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Biology of the Tobacco Hornworm in the Southern Cigar-Tobacco District[1]

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SUMMARY

The tobacco hornworm (*Protoparce sexta* (Johan.)) is one of the most common and destructive pests of tobacco in the United States. Undoubtedly the greater part of the $25,530,000 estimated annual damage to the tobacco industry brought about by hornworms is caused by this species. In the southern cigar-tobacco district it has been recognized as a pest of tobacco at least since 1850. It is par-ticularly injurious to cigar-wrapper and cigar-binder tobaccos, since the holes eaten in the leaves greatly reduce the quality of the product.

Wild host plants of the larvae are of little importance in the area, and tobacco is the preferred cultivated host. Host plants of adults

include a number of night-blooming flowers with tubular corollas.
The adults are active only at night and remain concealed during the day. Observations indicate that they mate only once. Feeding has been observed to precede oviposition under cage conditions. Experiments conducted in 1940 show that oviposition can take place in the absence of all food but that feeding increases the rate of oviposition.

Oviposition records from 164 captive females ranged from 1 to 1,133 eggs per female, with an average of 254. The seasonal average for females completing the larval period in the field was 255 eggs in May, 355 in June and July, and 198 in August and early September. The ratio of the number of eggs deposited (in cages) on the lower surface of the leaf to the number deposited on the upper surface was approximately 2 to 1. The preoviposition period averaged 1.8 days, the oviposition period 6.4, and the postoviposition period 1.5.

Under field conditions the number of eggs deposited on individual plants during the entire growing season ranged from 0 to 74, the largest and most vigorous plants receiving the most eggs. The ratio of the number of eggs deposited on the lower surface of the leaf to the number deposited on the upper surface is approximately 4 to 1, and practically no eggs are deposited on the stems of the plants. The greatest numbers of eggs are deposited on the upper third of the tobacco plant. There is no significant difference between the number of eggs deposited at the edges and the number deposited at the center of an open field of tobacco. This is true also of the number of eggs deposited adjacent to and at a distance from woods or other cover.

Heavy rains accompanied by lower temperatures reduce the number of eggs deposited. No evidence was obtained of any relationship between moonlight and the oviposition rate.

In 5,630 observations, the average incubation period was 4.9 days. No relationship between humidity and the length of the incubation period was noted, but there is a high inverse correlation between temperature and the length of the period.

Only 79 percent of the eggs deposited in cages were observed to hatch, whereas 95 percent of those collected from the field hatched.

Measurements of the area of tobacco leaf eaten show that there is an enormous increase in food consumption during the larval period. The size of the larva also increases greatly, almost doubling in each instar. The length of the larval period, as determined from 1,308 observations, ranged from 13 to 44 days, with an average of 20. The average length of the instars was as follows: First instar 3.4 days, second instar 2.9, third instar 3.0, fourth instar 3.9, fifth instar 6.6, and sixth instar 5.7. The normal number of instars is 5. There is no direct relationship between humidity and the length of the larval period, but there is a high inverse correlation between temperature and the length of the period. The length of the larval period averaged 3 days less under field conditions than it did in the insectary.

The average depth of pupation, as determined from 1,491 observations, was 5.5 inches. The length of the prepupal period ranged from 3 to 8 days in 2,727 observations. The length of the pupal period ranged from 14 to 738 days, with an average of 137. The percentage of individuals surviving hibernation ranged from 20 to

53. The indications are that even the lowest winter temperatures of the area have no effect on winter mortality.

The total length of the developmental period ranged from 33 to 441 days, with an average of 162 days, but pupation records from seasonal-history cages indicate that in a limited number of cases the developmental period may require about 2½ years.

The average life of the female is approximately 2 days longer than that of the male.

Approximately 48 percent of the adults observed were females.

The earliest appearance of adults in the spring is usually from the middle to the latter part of April, while the latest occurrence in the fall is from the latter part of October to the first of November. The latest individuals recorded are usually in the egg or larval stages.

Three complete generations and one partial generation a season are known to occur, and it appears that under favorable conditions four generations may be completed.

The seasonal abundance of all stages usually reaches a peak during July. This is followed by a sharp decrease about the first of August; from then on, very few individuals are present. An unseasonable reduction and termination of adult emergence is responsible for this scarcity, and the result is that there is a close correspondence between the seasonal history of the hornworm and the tobacco-growing season.

Predaceous wasps (*Polistes fuscatus* (F.) and *P. fuscatus* var. *metricus* Say), a small green spider (*Peucetia viridans* (Hentz)), and a small plant bug (*Cyrtopeltis varians* (Dist.)) attack the eggs and larvae. A number of common birds also attack the larvae, and the pupae are eaten by skunks and moles. The principal parasite is a fly (*Sturmia protoparcis* (Towns.)). *Apanteles congregatus* (Say) is of minor importance, although it is the most important parasite in other areas. A bacterial disease, apparently caused by *Bacillus sphingidis* (White), is sometimes prevalent. None of the natural enemies of the hornworm are of much value in direct control, but they do keep the population within certain limits.

INTRODUCTION

The tobacco hornworm (*Protoparce sexta* (Johan.)) is one of the most common and destructive pests of tobacco and tomatoes in the United States and is particularly harmful when it attacks cigar-wrapper tobacco.

Intensive biological studies on the insect were conducted at Quincy, Fla., from 1936 to 1941, inclusive. The main purpose of these investigations was to obtain information which might be of value in improving existing control measures against this pest. Although the data were affected by climatological and other factors existing in the area, in general the information obtained is applicable wherever this insect is a tobacco pest. This bulletin contains the complete results of the investigations, together with data accumulated by the junior author over a period of approximately 20 years prior to 1936. A preliminary account of the studies was published in 1938 (*19*).[4]

4 Italic numbers in parentheses refer to Literature Cited, p. 50.

Numerous references to the tobacco hornworm occur in the economic and taxonomic literature, but little has been published previously on its biology. Papers dealing largely with this subject have been written by Alwood (*1*), Garman and Jewett (*6*), and Gilmore (*8*).

HISTORY AND ECONOMIC IMPORTANCE

The original home of the tobacco hornworm appears to have been South America and, according to Webster (*29*), the diffusion northward probably took place either through the Windward and Leeward Islands and the West Indies, or through Panama, Honduras, and Cuba to Florida, and through Central America and Mexico to the western part of the United States. Its importance as a tobacco pest probably antedates the written history of the Western Hemisphere, since Garner et al. (*7*) state that tobacco was being grown from Canada to southern Brazil at the time of the discovery of America.

That the tobacco hornworm was well known to the colonial tobacco planters of Virginia and Maryland is shown by the frequent references to damage and control methods which appear in the early writings on tobacco culture. Although there is no way of determining from these references whether *Protoparce sexta* or the closely related tomato hornworm (*P. quinquemaculata* (Haw.)) was the species involved, it appears safe to assume that a large share of the damage was being caused by *P. sexta*. Probably the earliest official recognition of hornworm damage to tobacco is contained in the First Maryland Inspection Law, October 1640, which is quoted by Wyckoff (*31, p. 52*) as follows: "Bad tobacco shall be judged ground leafes (Second Crops leafs) notably brused or worm eaten."

The majority of the earliest references to the tobacco hornworm by economic entomologists appear in the publications of Walsh and Riley during the period from 1865 to 1893.

Stoutamire (*25*) states that tobacco has been cultivated in Florida for more than 100 years, and according to Tisdale (*26*) the industry reached considerable importance in Gadsden County during the period from 1830 to 1860. Commercial cultivation was almost discontinued for about 25 years following the Civil War, but a revival, made possible mainly by the development of artificial shade, took place in 1896, and production has been continuous since that date.

The recognition of the tobacco hornworm as a pest of tobacco in this area as early as 1850 is indicated by Glover (*10, p. 66*), who reports that about that time tobacco growers near Mount Pleasant, Fla., were placing cobalt in the blossoms of jimsonweed (*Datura stramonium* L.) to destroy the adults. The species became such a pest of tobacco in the State by 1895 that a study of this and other tobacco insects was undertaken by Quaintance (*22*).

The economic importance of the tobacco hornworm as a pest of tobacco is intensified by the fact that the leaves eaten are the marketable portion of the crop. Thus damage through loss in weight is to be expected, and in the case of the cigar-wrapper and cigar-binder types a further reduction in value results from the presence of the holes eaten in the leaves, since this lowers the quality of the product. Hyslop (*14, p. 45*) estimates the annual damage to the tobacco

industry in the United States by *Protoparce sexta* and *P. quinque-maculata* at approximately $25,530,000, and undoubtedly *P. sexta* is responsible for the greater portion of this damage. Damage to tomatoes, eggplants, peppers, and potatoes also adds materially to the total losses caused by this pest.

It would be practically impossible to produce the open-field types of tobacco without employing the most rigorous control measures against this pest (fig. 1). The cloth walls and tops of the shade structures usually afford a certain degree of protection to cigar-wrapper tobacco by preventing the entrance of ovipositing females from outside areas. However, even in the shade fields it is necessary to devote much expense and effort to hornworm control.

FIGURE 1.—Cigar-binder tobacco damaged by the tobacco hornworm. The plot on the right was treated with insecticides on a regular schedule throughout the season; the plot on the left was an untreated check.

DISTRIBUTION

The tobacco hornworm occurs over the greater part of the United States, the West Indies, Mexico, Central America, and parts of South America. The extreme northern and southern limits of its range are found in southern Canada and southern Brazil.

Information obtained through correspondence with State ento-mologists and from records compiled by the Insect Pest Survey of the United States Department of Agriculture indicates that the species has been reported from every State in the Union with the exception of Colorado, Montana, Washington, and Wyoming, and a detailed survey would doubtless reveal its presence in these States also.

In Mexico, *Protoparce sexta* has been recorded from Cordoba, in the State of Veracruz; Lampazos, in the State of Nuevo Leon; and Mazatlán, in the State of Sinaloa, but according to Hoffmann (*12, p. 217*) it occurs throughout the entire country. In the West Indies

it is known to occur in Barbados, Cuba, Jamaica, Puerto Rico, Dominican Republic, Trinidad, and the Virgin Islands. In Central America it is recorded from Nicaragua and Panama, and in South America from Brazil, Ecuador, and Uruguay. It also is reported to occur on the Island of Bermuda, and occasional specimens have been recorded from southern Ontario.

Rothschild and Jordan (*23, p. 68*) recognize four distinct geographical races or varieties: *Protoparce sexta sexta* (Johan.) from Canada to Honduras westward to the Pacific, *P. sexta jamaicensis* (Butler) from the West Indies, *P. sexta paphus* (Cramer) from Costa Rica to Argentina, and *P. sexta caestri* (Blanchard) from Chile.

Individuals apparently have become localized in the southern cigar-tobacco district, as there is no evidence of migration into or out of the area.

SYNONYMY[5]

The tobacco hornworm has been treated in the literature under a number of scientific names. The species was originally described as *Sphinx sexta* by Johansson (*15, p. 27*) in a thesis presented before the medical faculty of the Royal Academy, Uppsala, Sweden. The following year it was redescribed by Linnaeus (*17, p. 346*) as *Sphinx carolina*, and this specific name has persisted until comparatively recent times. A list of the original synonymy is as follows:

Sphinx sexta Johansson, 1763	*Sphinx afflicta* Grote, 1865
Sphinx carolina Linnaeus, 1764	*Sphinx lycopersici* Boisduval, 1875
Sphinx paphus Cramer, 1779	*Sphinx tabaci* Boisduval, 1875
Sphinx caestri Blanchard, 1854	*Protoparce griseata* Butler, 1875
Sphinx nicotiane Ménétries, 1857	*Protoparce jamaicensis* Butler, 1877
Sphinx eurylochus Philippi, 1860	

Much confusion has arisen with respect to the correct generic name of the species, some writers placing it under *Phlegethontius* and others under *Protoparce*.

The genus *Sphinx* was erected by Linnaeus (*16, p. 489*) and included all the then-known forms belonging to the present families Sphingidae, Aegeriidae, and Pyromorphidae. The genera *Phlegethontius* and *Cocytius* were erected by Hübner (*13, p. 140*) in 1819 as divisions of the original genus. In this division *jatrophae* (F). was included under *Cocytius*, and *cluentius* (Cramer) under *Phlegethontius*. The proper separation of species would have placed both in the same genus. Rothschild and Jordan (*23, p. 52*) cite *antaeus* (Drury) (with *jatrophae* as a synonym) as the type of *Cocytius*. While *antaeus* was not originally included in the genus by Hübner, *jatrophae* was included and should be considered as the designated type. In the same paper Rothschild and Jordan cite *cluentius* as the type of *Phlegethontius*, and as *cluentius* and *jatrophae* are congeneric they suppress *Phlegethontius* as a synonym of *Cocytius*. In 1856 Burmeister (*2*) erected the genus *Protoparce* for *rustica* (F.), which he redescribed, and he also listed five other species as belonging to the new genus. As none of these species are congeneric with *rustica*, all authors, so far as is known, consider this species as

the type of *Protoparce*. Furthermore, Butler (*3, p. 606*) definitely
cites *rustica* as the type of the genus. Therefore, since *sexta* is
congeneric with *rustica* it should be placed under *Protoparce*.

DESCRIPTION OF THE STAGES

THE EGG

The egg (fig. 2) is usually oval, although slight variations occur
and some eggs may be nearly spherical. The surface is smooth, and
the color varies from light green, when first deposited, to yellow, and
finally to white just prior to hatching. The average length is about
1.5 mm. and the average width about 1.25 mm.

FIGURE 2.—Eggs and newly hatched larvae of the tobacco hornworm on a
tobacco leaf. × 4. (Photo by J. G. Pratt.)

THE LARVA

The larva (fig. 3) has a cylindrical body, which is densely covered
with fine hairs. Biting mouth parts are present in all instars, and
there are three pairs of true legs on the thoracic segments and a
pair of prolegs on the third, the fourth, the fifth, the sixth, and the
last abdominal segments. The prothorax bears one pair of spiracles,
and there are eight additional pairs on the first eight abdominal
segments. The eighth abdominal segment is tipped with a dorso-
caudal horn, which is nearly as long as the body of the newly
hatched larva, having attained its full length at that time. The horn
is almost scarlet in the mature larva.

Newly hatched larvae are yellowish white, but after a short period of feeding the color changes to light green and the segments are demarked by faint white lines. Faint oblique, white stripes on the caudal portions of the pleura first appear in the second instar, and the black stripes associated with them become visible in the third instar. The whitish tubercles on the dorsal surface of the body also
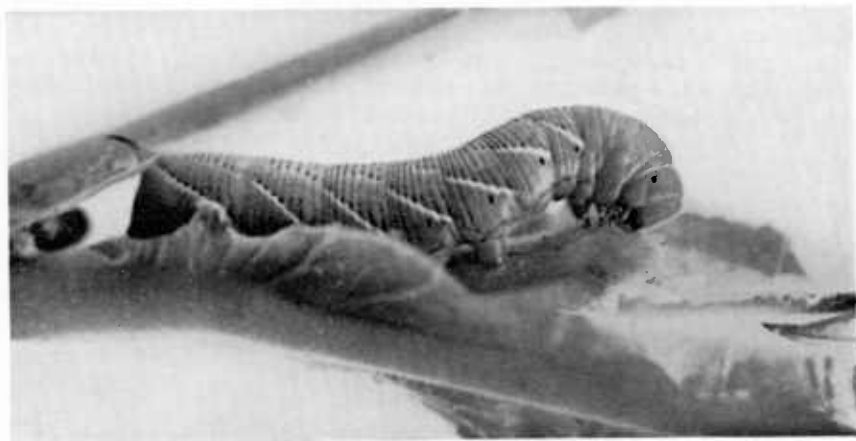

FIGURE 3.—Full-grown larva of the tobacco hornworm. Natural size.

become distinct in the third instar, and the spiracles are apparent to the unaided eye. The oblique, black and white stripes on the pleura become very distinct in the fourth instar, and the general color and appearance closely resembles that of the full-grown larva.

The full-grown larva is usually green, with seven oblique, black and white stripes on each side of the first seven abdominal segments. However, considerable variation in the body coloring occurs, although the stripes usually remain constant. Coloration varying all the way from green through various shades of dark green to black has been observed. In some cases the body may be covered with alternating, narrow, black and light-green bands, giving the larva a dark-gray appearance. The head capsule in such individuals is black, marked with fine, white spots, and the spiracles are surrounded with light-brown areas. A few specimens have been observed with bodies almost completely black, spiracles bordered with pink, and a narrow pink stripe associated with each of the oblique white stripes on the pleura. Similar color variations in the larvae of (*Sphinx*) *Protoparce quinquemaculata* are discussed by Lintner (*18, p. 648*).

THE PUPA

The pupa (fig. 4) is of the obtect type, with the tongue case bent sharply backward, the tip touching the sternum about one-third of the distance from the base to the end of the abdomen. The wings extend about one-half the distance to the posterior end of the body. When first formed, the pupal case is bright yellowish green, but

during the succeeding 24 hours this color changes to light brown, and usually at the end of the second day the final dark brown has been assumed.

FIGURE 4.—Pupa of the tobacco hornworm. × 2.

THE ADULT

The adult (fig. 5) is a moderately large moth with a wing expansion of from 76 to 127 mm. The general color of the dorsal surface of the body and forewings is dark brownish gray. The thorax is marked with several white spots, which are ringed with black. The forewings have a somewhat variegated appearance, owing to the presence of a number of wavy, dark-brown, transverse bands. There is a broad white spot at the base of each forewing, and a smaller white spot at the end of each discal cell. The outer margins of the forewings are fringed with short, dark-brown scales, among which several tufts of white occur. The hind wings are darker, and are traversed by a number of broken, oblique cross bands of white and dark-brown scales. A short fringe of whitish scales occurs on the outer margins. This fringe is spotted with brown.
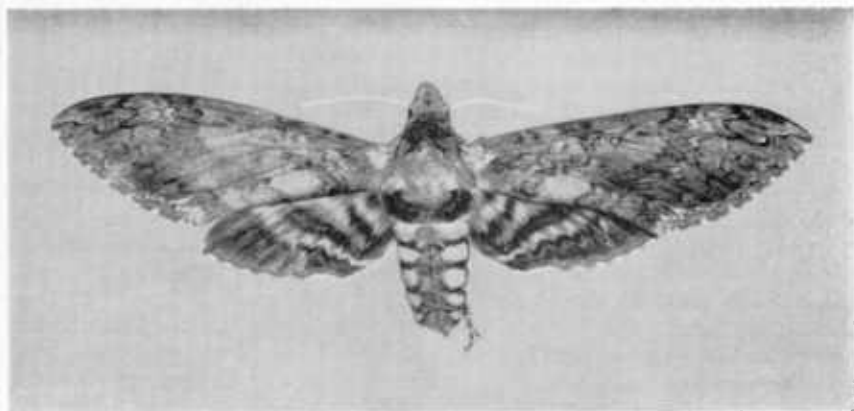

FIGURE 5.—Adult of the tobacco hornworm. Natural size.

Two lateral black spots occur on the dorsal surface of the base of the abdomen, and the six succeeding segments are marked with six pairs of orange spots. These become progressively smaller toward the tip of the abdomen, and each pair is associated with a pair of median white spots. The number of orange spots is not always constant, and occasional specimens have five pairs instead of the normal six.

The ventral surface of the wings is light brownish gray and is crossed by a few bands of darker brown. The ventral surface of the body is gray, with three or four median, dark-brown spots on the abdomen. The palpi and the ventral surface of the thorax are heavily clothed with long hairs.

The males are usually smaller than the females, but are similar in appearance, the main apparent structural difference being in the antennae. The antennae of the male are much larger and more complex than those of the female.

RELATED SPECIES

Thirty-five species are listed in Lepidopterorum Catalogus (*28, pp. 32-44*) under the genus *Protoparce*, and five of these are native to the United States. However, only *Protoparce sexta*, *P. rustica*, and *P. quinquemaculata* occur in the southern cigar-tobacco district. *Protoparce occulta* (Rothschild and Jordan) is recorded from Texas and Arizona, while *P. brontes* (Drury) is supposed to occur in southern Florida.

The adult of *Protoparce rustica* is a large, heavy-bodied moth with a wing expansion of about 121 mm. In general color the body and wings are dark brown, spotted with white, the white markings forming a definite wavy pattern toward the outer margins of the forewings. From 6 to 10 orange-yellow spots occur on the sides of the abdomen. The ventral surface of the body is almost completely white. The appearance of the larva is unknown to the writers. Food plants of the species are listed as *Bignonia*, etc. (*4, p. 609*). Only a few adults occur each season.

The tomato hornworm (*Protoparce quinquemaculata*) is often confused with the tobacco hornworm, since their appearance, habits, and food plants are similar. These two species, however, are readily distinguishable. The adult of *P. quinquemaculata* is ashy gray, and there are five pairs of orange-yellow spots on the sides of the body, instead of six as in *sexta*. The tongue case of the pupa is longer in *quinquemaculata*, and in the larva each of the eight oblique stripes on the sides of the body joins a horizontal stripe at its lower end, forming a series of V's. Also, the posterior horn on the larva is black, instead of red as in *sexta*.

Protoparce quinquemaculata is more northern in its distribution, its range extending from southern Canada to the southern part of the United States. In Canada and the northeastern part of the United States it is an important pest of tobacco, but its abundance decreases the farther south it occurs, and it is of no economic importance in the southern cigar-tobacco district. Trapping records from 1937 to 1940, inclusive, show that over nine times as many *P. sexta* adults were captured as adults of *P. quinquemaculata*. Further-

more, thousands of larvae were collected in the field each season, but only an occasional larva of *P. quinquemaculata* was found, indicating that the species does not breed readily in this area. This conclusion is substantiated by the fact that no eggs could be obtained from a number of caged pairs. It appears, therefore, that the southern cigar-tobacco district represents the southern limits of the range of *P. quinquemaculata.* However, Hoffmann (*12, p. 217*) states that it occurs in the northern and central parts of Mexico. Quaintance (*22*) states that in the Florida Agricultural Experiment Station collection there were six times as many *P. sexta* (*P. carolina*) as *P. quinquemaculata* (*P. celeus*).

HOST PLANTS

So far as known, larvae of the tobacco hornworm in the district under consideration feed only on plants belonging to the family Solanaceae.

During the seasons of 1937, 1938, and 1939 observations were made to determine the extent to which the tobacco hornworm occurs on wild host plants in the area. The plants examined included jimsonweed (*Datura* sp.), groundcherry (*Physalis angulata* L.), black nightshade (*Solanum nigrum* L.), and horsenettle (*S. carolinense* L.). It was found that, with the exception of jimsonweed, all the plants were extremely scarce. The average number of eggs per plant was only 0.26, and larvae were found on none of the plants except jimsonweed and horsenettle. Furthermore, not a single record was obtained of a larva completing its development on any of the plants. These records show that the importance of wild host plants in the biological complex of the species in the southern cigar-tobacco district is practically negligible.

Tomatoes, eggplants, peppers, and potatoes are among the cultivated Solanaceae other than tobacco attacked by hornworm larvae. Potatoes are produced on a number of acres in the vicinity of Quincy, Fla., but the crop is planted during the fall and winter, and usually reaches maturity just after the beginning of the hornworm season. Tomatoes, eggplants, and peppers are grown commercially on a limited acreage, and a few plants are produced for home consumption.

General observations and records made during the seasons of 1936, 1937, and 1938 indicated that tobacco was greatly preferred as a host plant over tomatoes, eggplants, and peppers. This was shown by the comparative numbers of eggs deposited on each type of plant. In 1940 an experiment was conducted in which 15 plants each of tobacco, tomato, eggplant, and pepper were grown in the same field. The eggplants and peppers were transplanted early enough so that they would mature at the same time as the tobacco and tomatoes; consequently, the foliage of all the plants was in approximately the same condition throughout the deposition period. Egg counts were begun on May 30 and concluded on August 10. The total number of eggs on each type of plant was as follows: Tobacco 677, tomato 141, eggplant 216, and pepper 168. This shows that tobacco is about three times as attractive as eggplant, and about four or five times as attractive as tomato or pepper.

The adult tobacco hornworm feeds on a number of night-blooming flowers with tubular corollas. Feeding on the blossoms of the following plants has been recorded during the course of these investigations: Jimsonweed (*Datura* sp.), petunia (*Petunia* sp.), four-o'clock (*Mirabilis jalapa* L.), evening-star (*Nicotiana alata* var. *grandiflora* Comes), tobacco (*N. tabacum* L. and *N. repanda* Willd. ex Lehm.), swamp lily (*Crinum* sp.),[6] and mimosa (*Albizzia julibrissin*) (Willd.) Durazz.),[7] an ornamental tree which was naturalized from Asia, according to Small (*24, p. 653*).

In addition to several of the above plants, Gilmore (*8, p. 709*) records feeding on flowers of western catalpa (*Catalpa speciosa* Warder), wild potato vine (*Ipomoea pandurata* (L). G. F. W. Mey), trumpetcreeper (*Bignonia radicans* L.), common evening-primrose (*Oenothera biennis* L.), daylily (*Hermerocallis* sp.), mallow (*Hibiscus lasiocarpus* Cav.), honeysuckle (*Lonicera* sp.), and hollyhock (*Althaea rosea* (L.) Cav.).

CONDITIONS AFFECTING THE INVESTIGATIONS

Although the life history, habits, and seasonal abundance of the tobacco hornworm, as related in this bulletin, were influenced by the conditions existing in the vicinity of Quincy, Fla., where the studies were made, in general the data are applicable wherever the insect is a pest of tobacco. Quincy lies in the southwestern part of the Florida-Georgia tobacco-growing area, which is referred to in this bulletin as the southern cigar-tobacco district. In most of this area the flue-cured cigarette type of tobacco is grown, but in this district, which covers the greater part of Gadsden County, Fla., and adjoining Decatur County, Ga., cigar types of tobacco have been of major importance. During 1941 (*27*) about 4,000 acres of tobacco was grown under cheesecloth or lath shades for use as cigar wrappers, with a farm value of over 2 million dollars, while on more than 1,000 acres cigar-binder tobacco and some cigarette tobacco was grown in open fields.

The southern cigar-tobacco district lies in the Gulf Strip of the Lower Austral life zone, as established by Merriam (*21*). The temperature is neither extremely high in summer nor exceptionally low in winter, while the annual rainfall is sufficient to maintain a rather high humidity during the greater part of the year. The normal rainfall is 54.02 inches annually, and the normal mean temperature is 67.60°F. The temperature and precipitation were about normal during 1936 and 1939, whereas 1937 was characterized by an excess rainfall of 12.15 inches, 1938 by a deficiency of 12.17 inches, and 1940 by an abnormally cold winter.

Most of the soil of Gadsden County is classed by Henderson (*11*) under the general heading of Norfolk-Red Bay and Marlboro-Greenville groups. The chief cigar-tobacco soils under these general groups are the Orangeburg and Magnolia series, and it is in such soils that most of the pupation of the tobacco hornworm occurs. In the Orangeburg series the first layer of 4 inches consists of brownish-gray to

grayish-brown loamy sands. The next layer of 12 inches is composed of yellow to brownish-yellow loamy sand, and the subsoil is red friable sandy clay. In the Magnolia series the soil is similar, though somewhat thinner, and the subsoil is heavier.

LIFE HISTORY AND HABITS

ACTIVITIES OF THE ADULTS

The adult of the tobacco hornworm is active only at night. Observations under cage conditions indicate that there are two periods of activity, the first being from about 7:30 to 9 p. m. and the second from about 4:30 to 5:30 a. m. These periods correspond roughly to the hours of evening and morning twilight. However, records were obtained of adults remaining active all night in the field. This agrees with the observations of Gilmore (8).

The moths are strong fliers, but flight is erratic, and no great distance is covered in a straight line. Gilmore (8) reports that the maximum distance covered was 1¼ miles, and this was recorded on the second day after release.

Almost immediately after taking flight in the evening, the adult begins feeding, and observations have shown that under cage conditions feeding always precedes oviposition. Experiments to determine the effect of food on the oviposition rate were conducted during the season of 1940. Four large, cloth-covered cages were used in these studies, and the food conditions were varied as follows: Cage 1, jimsonweed blossoms plus dextrose-water solution; cage 2, jimsonweed blossoms; cage 3, water; cage 4, neither food nor water. Oviposition records were obtained from a total of 30 females, this number being divided as equally as possible among the four cages. The average oviposition rate was 221 eggs in cage 1, 290 in cage 2, 164 in cage 3, and 161 in cage 4. This shows that while feeding tends to increase the rate of oviposition, females are able to oviposit even without food or water.

Mating occurs while the moths are at rest on some support. As soon as union is completed, the pair face in opposite directions and hang vertically downward, the female being above and the male below. One pair remained in coitus for 4 hours and 55 minutes. Mating was observed only twice during the course of the investigations. The comparatively few times that mating has been observed and the rather prolonged period of coitus leads to the conclusion that it occurs only once during the life of the adult. The indications are that mating usually takes place about 11 p. m. on the day of emergence.

Cage observations indicate that practically all oviposition takes place before 9 p. m. Oviposition occurs while the female is poised over the tobacco leaf, this position being maintained partly by clinging to the leaf with the legs and partly by a rapid motion of the wings, the tip of the abdomen being curved forward and upward at the same time (fig. 6).

Adults remain hidden during the daytime in some secluded spot. It has been the belief that such shelter is sought against the bark of trees. This is probably true, but repeated examinations (from the

ground level) of various types of trees adjoining open fields of tobacco have failed to reveal the presence of a single individual. Occasionally a moth was found on the under side of a tobacco leaf, and even more rarely on a cornstalk, but the diurnal hiding place of the majority of individuals was not discovered.
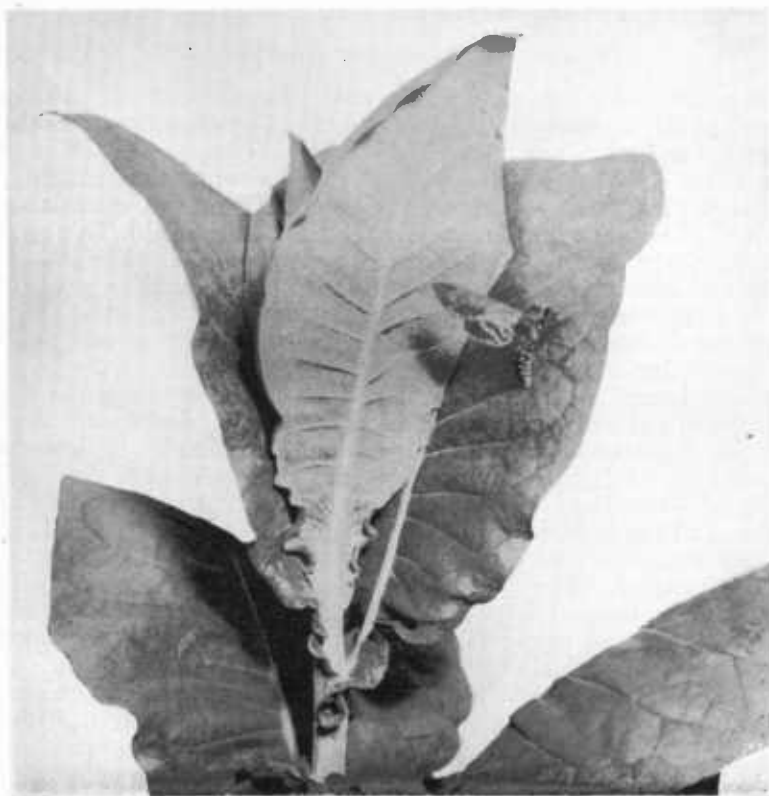
FIGURE 6.—Tobacco hornworm ovipositing on a tobacco plant.

OVIPOSITION UNDER CAGE CONDITIONS

Oviposition studies were conducted from 1936 to 1939, inclusive, by recording the number of eggs obtained daily from mated females confined to cloth-covered cages. The cages originally constructed for this purpose were grouped in a rectangular block. Cloth partitions divided the block into 12 compartments, each 6½ by 6 feet by 6½ feet, and a canopy of dark cloth suspended 1½ feet above the top shielded the interior from the direct rays of the sun (fig. 7). A wooden post about 3 feet high was fixed in the center of each cage, and a small cylindrical tin can with holes punched in the cover was placed on the top of each post. These tins were kept full of fresh water, and every evening jimsonweed blossoms were placed in the holes in the covers. To provide additional nourishment, a few drops of dextrose-water solution (1 gm. of dextrose to 20 ml. of water)

were placed in each blossom. Oviposition stimulus was provided by one or two potted tobacco plants in each cage. The majority of the eggs were deposited on these plants, although occasionally some were placed on the sides of the feeding tins or on the tops and walls of the cages.

Observations soon showed that these cages were not satisfactory. The interiors were so small that the moths spent a large part of the time they were active trying to escape, and the potted tobacco plants apparently did not attain sufficient vigor and succulence to

FIGURE 7.—Small group cages used in oviposition studies on the tobacco hornworm.

furnish the proper oviposition stimulus. To remedy this situation, six larger individual cages were constructed prior to the 1937 season. These cages were 14 by 14 feet by 9 feet (fig. 8), and each contained two tobacco plants growing in the soil of the bottom of the cage. The feeding arrangements and the method of obtaining the oviposition records were the same as those employed in the smaller cages.

Normally, a pair of moths was placed in each cage, but occasionally several males were placed with one female. However, no attempt was made to determine what effect this might have on the rate of oviposition, since it was found that mating took place through the walls of the cages, thus making it difficult to obtain accurate records on pairing.

A summary of the oviposition records obtained is presented in table 1. The rate per female ranged from a minimum of 1 to a maximum of 1,133, with an average of 254. This average, however, is abnormally low, owing to the effect of the records obtained from the small cages. A more reliable average of 271 eggs per female was calculated from the records obtained in the large individual cages. Female moths used in these studies were obtained from two sources, (1) from larvae reared in the insectary and (2) from larvae collected in the field. Those from the field larvae were more prolific, and the 3-year average of such individuals is 302 eggs per female, as compared with 202 for individuals reared in captivity.

FIGURE 8.—Large individual oviposition cages used in life-history studies of the tobacco hornworm.

TABLE 1.—*Average oviposition records of the tobacco hornworm under cage conditions. Quincy, Fla., 1936–39*

Year	Type of cage	Moths	Average pre-oviposition period	Average oviposition period	Average post-oviposition period	Average eggs per female
		Number	*Days*	*Days*	*Days*	*Number*
1936	Small group cages	14	3.8	7.6	0.6	193
	Large individual cages	5	2.8	6.4	0	320
1937	Small group cages	9	1.6	4.2	1.6	96
	Large individual cages	51	1.9	6.9	1.6	309
1938	Large individual cages	42	1.6	6.0	1.9	251
1939	Large individual cages	43	1.4	7.4	1.8	238
1936–39		164	1.8	6.4	1.5	254.3

It was found also that females emerging early in the season deposited very few eggs, the average increasing to a peak by the latter part of June or early in July, and then declining throughout the remainder of the season. The 3-year average for females emerging in May is 255, in June and July 355, and in August and September 198. These averages are based on the records obtained from females which completed their larval development in the field. It appears, therefore, that normally the oviposition rate is about as follows: An average of approximately 250 eggs per female during the early part

of the season, increasing to 350 eggs per female in midseason, and decreasing to about 200 eggs per female during the latter part of the season, with a seasonal average of approximately 300 eggs per female. The rate is probably much higher under natural conditions. Gilmore (8) says that the average for captive females of this species in Tennessee was about 500 eggs.

The average preoviposition, oviposition, and postoviposition periods are shown also in table 1. The records obtained from the small cages are slightly abnormal, but they compare favorably with those obtained from the large cages. The averages for the four seasons are: Preoviposition period 1.8 days, oviposition period 6.4, and postoviposition period 1.5.

Previous workers have observed that the majority of the eggs are deposited on the under surface of the tobacco leaf, and Alwood (1) states that they are nearly always deposited there. To obtain comparative figures on the number of eggs deposited on the various parts of the tobacco plant and on the upper and lower surfaces of the leaves, the position of each egg was recorded. The results are shown in table 2. The ratio of the number of eggs deposited on the under surface of the leaf to the number deposited on the upper surface is slightly more than 2 to 1, whereas the number deposited on the stems of the plants is relatively insignificant. It appears that the abnormal leaf development of plants grown in cages was largely responsible for the deposition of such a large number of eggs on the upper surface of the leaf, as very different results were obtained under open-field conditions.

TABLE 2.—*Positions in which eggs of the tobacco hornworm were deposited by females caged with growing tobacco plants. Quincy, Fla., 1936–39*

Year	Eggs deposited in indicated positions				
	On upper surface of leaves	On lower surface of leaves	On stems of plants	On cages and feeding tins	Total
	Number	*Number*	*Number*	*Number*	*Number*
1936_____	6,505	16,293	117	307	23,222
1937_____	4,904	11,758	83	38	16,783
1938_____	4,198	6,377	10	35	10,620
1939_____	2,692	7,446	9	20	10,227
1936–39_____	18,299	41,874	219	400	60,852

OVIPOSITION UNDER FIELD CONDITIONS

Oviposition studies under field conditions were conducted during each of the five growing seasons from 1936 to 1940. The observations were made in open fields of tobacco to obtain records under more nearly natural conditions than would have been the case if shade fields had been utilized for this work. Preliminary observations in 1936 were carried on in one field only, but in each of the four succeeding seasons the number of fields was increased to six. Representative fields were chosen in each instance, and the locations were distributed in a rough circle covering 25 to 30 square miles and including a fairly typical section of the area. Egg counts were made twice a week in each field.

One thousand two hundred and sixty individual tobacco plants were under observation during the period, and 16,233 eggs were recorded, or an average of 12.9 eggs per plant (table 3). The number of eggs deposited on individual plants ranged from 0 to 74. This range, in part at least, is caused by the difference in the oviposition stimulus of the plants. In general, the largest and most vigorous plants receive the most eggs, and when wide variations in development occur, corresponding variations in the number of eggs deposited per plant may be expected. An illustration is furnished by the season record obtained at station 3, field 3, in 1938. The plants in this field varied greatly in size, owing to poor cultivation, and the total number of eggs recorded on each plant at station 3 is as follows:

Plant No.	Number of eggs	Plant No.	Number of eggs
1	0	6	0
2	4	7	0
3	6	8	0
4	11	9	3
5	21	10	5

Plant 5 was the largest and most vigorous throughout the season, and the other plants varied in size and vigor in accordance with the number of eggs recorded from each.

TABLE 3.—*Number and position of eggs of the tobacco hornworm deposited under field conditions. Quincy, Fla., 1936–40*

Year	Fields repre- sented	Plants observed	Eggs found per plant (average)	Eggs found at indicated positions on plants				
				On lower surface of leaves	On upper surface of leaves	On lower third of plant	On middle third of plant	On upper third of plant
	Number	*Number*	*Number*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
1936	1	60	3.1	65	35	9	33	58
1937	6	300	7.8	74	26	5	46	49
1938	6	300	15.0	76	24	5	39	56
1939	6	300	8.7	81	19	5	36	59
1940	6	300	22.0	80	20	2	38	60
1936–40	25	1,260	12.9	78	22	4	39	57

Cigar-filler, cigar-binder, and cigarette tobaccos were all included at one time or another in the oviposition studies, and an attempt was made to determine the relative attractiveness of these types to oviposition as shown by the number of eggs deposited on each. As replications of each type could not be obtained at every location, no conclusive evidence was obtained on this point. However, the indications were that the greatest number of eggs were deposited on cigar binder. Apparently this is so because the leaves of this type are thicker and more succulent than those of the filler type, and they remain in this condition for a longer period than do those of the cigarette type. The latter, while at least as attractive as those of the binder type during the early part of the season, reach maturity earlier and then become dry and unattractive.

To obtain a more natural record of the relative numbers of eggs deposited on the upper and lower surfaces of the tobacco leaf than was obtained under cage conditions, the numbers of eggs collected

from both surfaces were recorded. The results are shown in table 3. The ratio of the number of eggs deposited on the lower surface of the leaf to the number deposited on the upper surface was nearly 4 to 1. This record differs from that obtained under cage conditions and shows the distribution to be expected on tobacco growing normally in the field. Only 7 eggs in all were found on the stems of the 1,260 plants under observation. This relatively small number shows that deposition on the stem of the plant is by chance only.

To obtain information on the relative numbers of eggs deposited at different heights on the tobacco plant, a record was made of those deposited on each of the three vertical sections—the bottom, middle, and upper thirds. Obviously the sizes of these sections varied with the growth of the plant, and the limits of each were determined as closely as possible by inspection every time that counts were made. The results obtained by this method are presented in table 3. The fewest eggs were deposited on the lower third, the next greater number on the middle third, and the most on the upper third. The records show that the position of deposition varies progressively upward with the advance of the season. The first eggs are found almost exclusively on the lower and middle leaves. A few weeks later the majority are deposited on the middle leaves, and as the season advances most of the eggs are placed on the middle and upper leaves. The chief factor involved in this variation appears to be the progressive upward ripening of the leaves from the bottom to the top of the plant. The result is that the greatest number of eggs are placed always on the upper third of the plant, since the period of maximum egg deposition coincides with the period in which the upper leaves are in the most favorable state for oviposition.

In 1936 groups of 10 tobacco plants each were located in 6 fixed stations, 1 in each corner and 2 in the center of the field. The same arrangement was employed in each of the succeeding seasons, with the exception that only one station was located in the center of each field. Since a separate record of the number of eggs collected at each station was maintained, it is possible to make a comparison between the number of eggs collected at the edges of the fields and the number collected at the centers. The results are shown in table 4. The difference between the average numbers taken at the two locations is so slight that it is concluded that there is little difference between the number of eggs deposited near the edges and at the centers of open fields of a size ranging from 1 to 3 acres, which is typical of the area. During the early part of the season some tendency has been noted for the greatest number of eggs to be deposited on the side of the field nearest the principal hibernation point, but the distribution becomes more uniform as the season advances. A similar comparison was possible between corner stations located near woods and corner stations in the open, although a comparable number were located in both situations in 1937 and 1938 only. The average number of eggs collected from 19 stations located near woods was 117, as compared with an average of 113 collected from 29 stations in the open. Here again the difference is too small to be considered significant.

TABLE 4.—*Relative numbers of eggs of the tobacco hornworm deposited per plant near the edges and at the center of typical open fields of tobacco. Quincy, Fla., 1936–40*

Year	Eggs near the edges of the fields	Eggs at the centers of the fields
	Number	*Number*
1936	3.5	2.2
1937	7.5	9.2
1938	15.6	12.9
1939	8.4	9.0
1940	22.7	19.3
Average	11.3	10 5

FACTORS AFFECTING OVIPOSITION

In general, weather conditions appear to have little effect on oviposition. However, during rainy periods accompanied by a marked reduction in temperature an appreciable decrease in the oviposition rate has been recorded.

Many of the tobacco growers in the area maintain that the peak of egg deposition may be expected during the period of full moon in June, and it is the popular belief that this phenomenon is directly associated with the increased intensity of the moonlight at that time —that is, that moonlight is a direct stimulant to oviposition. Experiments and general observations were conducted in 1936, 1937. and 1938 to determine any possible relationship between the intensity and duration of moonlight and the deposition rate. This study was rather general, as a number of uncontrolled variants could not be eliminated without devoting full attention to this investigation. However, no evidence was obtained that would indicate the existence of any degree of correlation between moonlight and oviposition. The increase in egg deposition observed by the growers apparently is coincident with the period mentioned rather than dependent on it. In reality several other factors, including greater abundance of adults and emergence of females having a greater egg-laying potential, combine to produce the oviposition peak which occurs at about this time each season.

The fluctuations in oviposition produced by the condition and state of maturity of the tobacco plant have already been discussed.

INCUBATION

Eggs collected from the oviposition cages were placed on pieces of tobacco leaf and held in the insectary for hatching. Each lot of eggs was covered with an inverted jelly glass and kept under daily observation until hatching was completed. Records obtained in this manner are summarized in table 11 (p. 34). The average incubation period was 4.8 days in 1936, 5.2 days in 1937. 4.4 days in 1938, and 4.9 days in 1939, and the average for the four seasons was 4.9 days.

RELATIONSHIP OF HUMIDITY AND TEMPERATURE TO LENGTH OF THE INCUBATION PERIOD

The relative humidity in the insectary normally ranged from about 30 to 90 percent every 24 hours during dry weather. There usually was a gradual rise during the late afternoon and evening.

reaching the highest point about midnight.and remaining constant until about 6 o'clock in the morning. A gradual decrease occurred from that time onward, reaching the lowest point during the hottest part of the day. During wet weather the humidity generally remained at or near 100 percent continuously.

The effect of such fluctuations in humidity on the length of the incubation period could not be determined, since it was necessary to keep the humidity within the jelly-glass egg containers constantly near the saturation point to prevent the eggs from desiccating. This was accomplished by placing the bits of tobacco leaf bearing the eggs on pieces of blotting paper which were moistened with water frequently. It was found that hatching will occur only under conditions of constant high humidity. Garman and Jewett (6) made the same observation in the course of their investigations on the life history of the tobacco hornworm in Kentucky. Apparently the proper degree of moisture is obtained in nature through contact with the leaf of the host plant.

Temperature was found to have an appreciable effect on the length of the incubation period. Temperature records were obtained in the insectary by means of a hygrothermograph, which was checked frequently with a standard thermometer. The relationship between temperature and the length of the incubation period in 1936, 1937, 1938, and 1939 is shown in figures 9 and 10. Each point on the incubation curve corresponding to a given deposition date represents the average length of the incubation period of all eggs deposited on that date. Each point on the temperature curve is the mean temperature during the average incubation period after the date of deposition. As the eggs are deposited at night, the deposition date was excluded and the hatching date included in calculating the mean temperature. For example, the average incubation period for eggs deposited on July 24, 1936, was 4 days, and 86.5° F. is the point on the temperature curve for that date. This represents the mean temperature for the 4-day period from July 25 to July 28, inclusive. In the case of fractional averages, the mean temperature was calculated to the nearest number of whole days.

Although there is no great range in the length of the incubation period, the curves show that short incubation periods are dependent on high temperatures. There is a high degree of correlation between the mean temperature and the length of the incubation period in each of the four seasons. The correlation coefficients are −0.93 for 1936, −0.67 for 1937, −0.81 for 1938, and −0.75 for 1939. These are all highly significant.

HATCHING

When the larva is ready to emerge from the egg it proceeds to gnaw a hole through the side of the shell of sufficient size to permit the passage of the head capsule, which is much greater in diameter than the remainder of the body. After the hole is enlarged sufficiently, the larva emerges head foremost, uncoiling its body slowly as it moves out of the shell. Observations indicate that no feeding on the eggshell occurs after emergence, although Alwood (1) states that such feeding does occur.

FIGURE 9.—Incubation period of the tobacco hornworm as correlated with temperature. Each point on the temperature curve for a given date represents the mean temperature for the average incubation period of eggs deposited on that date. Quincy, Fla., 1936–37.

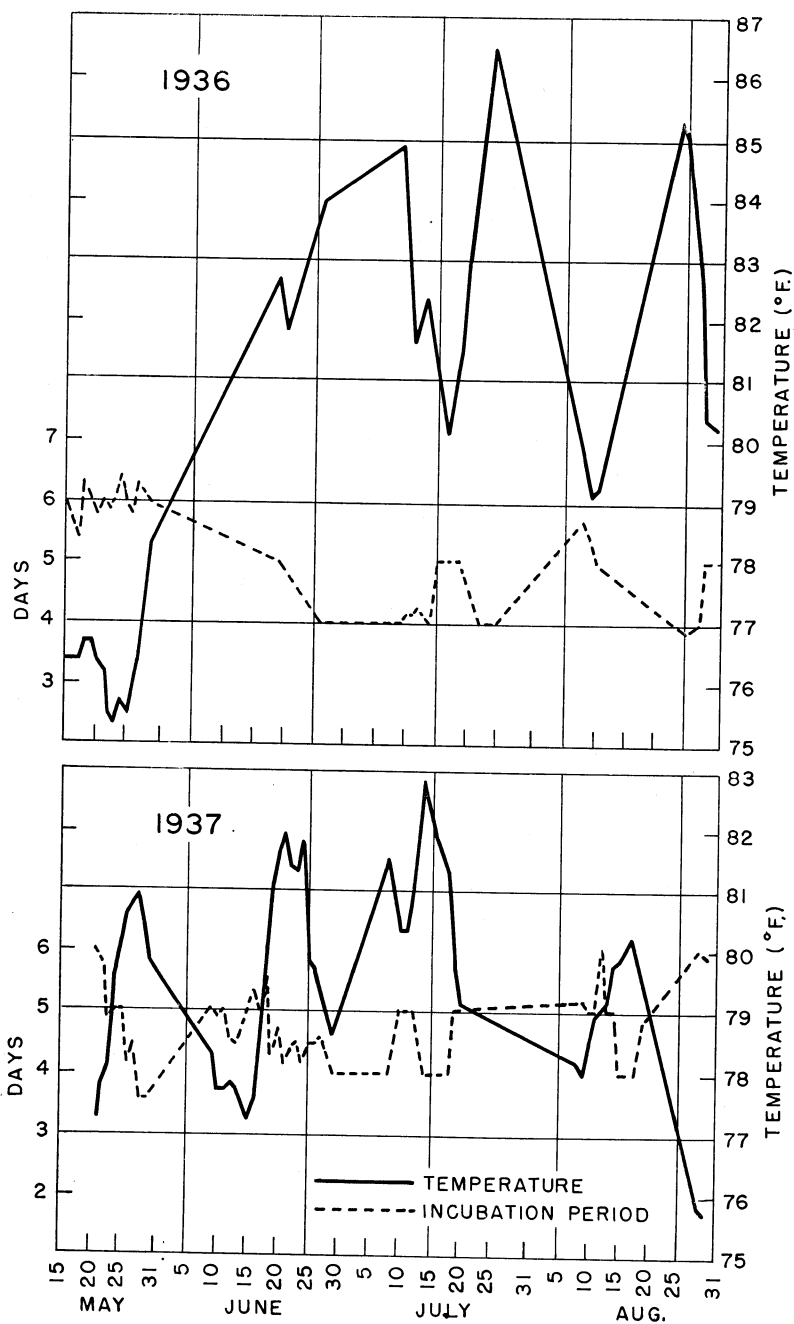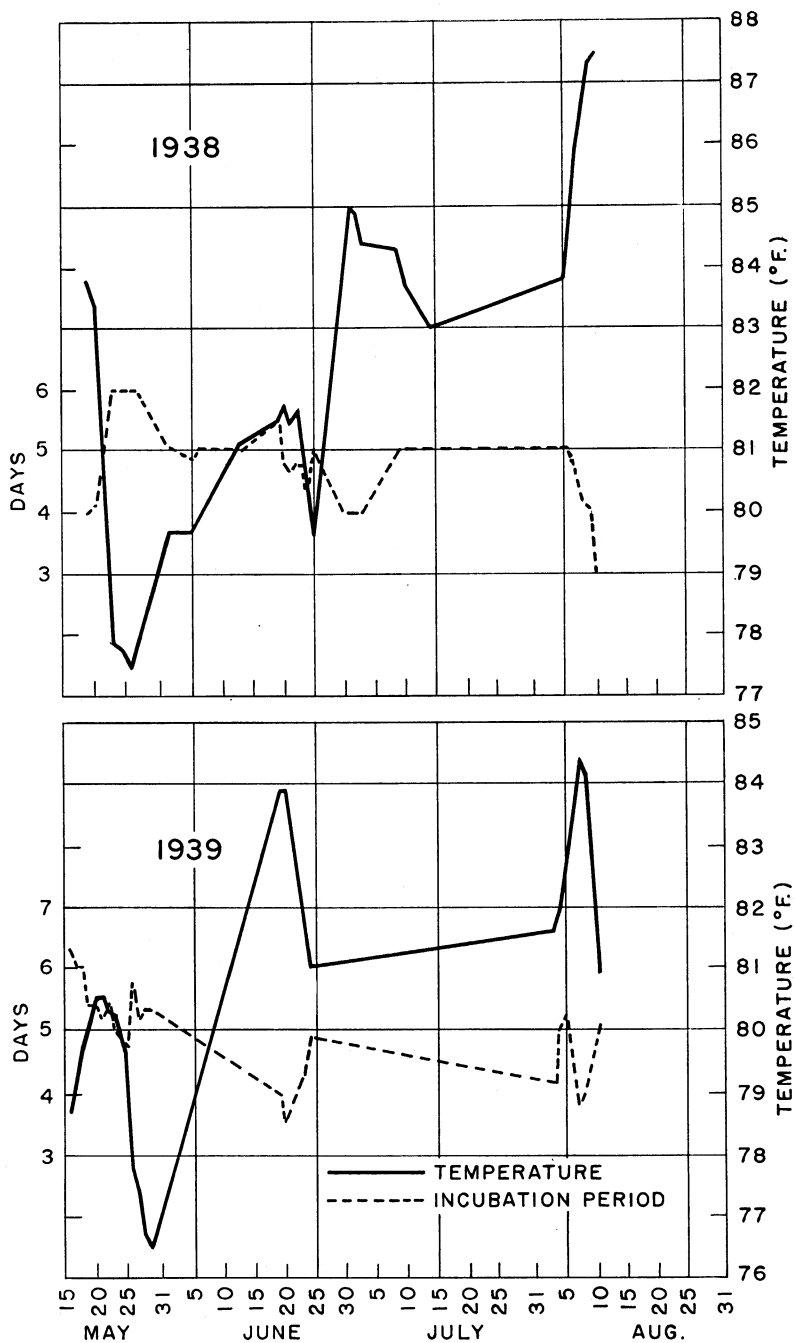FIGURE 10.—The incubation period of the tobacco hornworm as correlated with temperature. Each point on the temperature curve for a given date represents the mean temperature for the average incubation period of eggs deposited on that date. Quincy, Fla., 1938–39.

During the course of these investigations, records were kept on the viability of the eggs as determined by the percentage of hatch. For comparative purposes, such records were obtained from eggs deposited under both cage and field conditions. The results are presented in table 5. The total hatch for eggs deposited under cage conditions was 79 percent, as compared with a total of 95 percent for eggs deposited in the field. Thus it is apparent that nearly all the eggs deposited under natural conditions must be viable.

TABLE 5.—*Relative viability of eggs of the tobacco hornworm deposited under cage and field conditions. Quincy, Fla., 1936–39*

Year	Total eggs observed		Eggs that hatched	
	In cages	In the field	In cages	In the field
	Number	*Number*	*Percent*	*Percent*
1936	4,580	923	71	96
1937	3,825	1,227	75	93
1938	2,970	1,402	92	96
1939	2,439	626	86	95
1936–39	13,814	4,178	79	95

LARVAL STAGE

Newly hatched larvae eat small, round holes in the surface of the tobacco leaf at points considerably removed from the margins, and as development progresses they straddle the edges of these holes with their true legs and feed on the part thus brought beneath the anterior portion of the body. In feeding, the larva reaches as far forward as possible and cuts backward toward the legs with shearing motions of the mandibles. The larva repeats this operation continuously by moving forward around the edge of the hole as often as is necessary to bring additional leaf surface within reach. Full-grown larvae usually feed in the same manner astride the margin of the leaf. In all cases the greater part of the body remains concealed beneath the underside of the leaf. First instars spin a fine, adhesive thread, which prevents them from falling to the ground when they lose their footing. In later instars stout hooks on the prolegs hold the larvae firmly in place.

Feeding is almost continuous, except during the molting periods, which last about 24 hours. During these periods the larva remains quiescent on the under surface of the leaf. In molting, the head capsule splits at the point of junction with the thorax, and the larva works its way out of the old skin, which it leaves attached to the leaf.

There is an enormous increase in the amount of food consumed by larvae during the successive stadia. This increase is the greatest during the fifth or last stadium. Observations made at the Quincy laboratory in 1923 show the relative areas of leaf surface of cigar-wrapper tobacco eaten by larvae of each of the different instars. These data are presented in table 6. It may be seen from this table that the number of square inches of leaf surface eaten increases markedly with each succeeding instar, the amount being about 11 times as great for the fifth as for the fourth.

TABLE 6.—*The quantity of cigar-wrapper tobacco consumed by each instar of the tobacco hornworm. Quincy, Fla., 1923* [1]

Instar	Area of leaf consumed		
	Maximum	Minimum	Average
	Square inches	*Square inches*	*Square inches*
First	2.9	0.3	0.8
Second	5.7	.4	1.5
Third	7.2	2.7	5.2
Fourth	48.6	18.0	27.2
Fifth	469.2	146.7	301.0
First to fifth, inclusive	533.6	168.1	335.7

[1] Data obtained by J. N. Tenhet. The figures represent the average area of leaf surface consumed by 10 larvae.

A similar increase in the size of the larva occurs during the developmental period. Measurements were made of the length and width of the body and the width of the head capsule of larvae reared in the insectary. All larvae utilized were killed just prior to molting, or after the full size for each instar had been obtained. The measurements are shown in table 7. It will be noted that the increase in size is not directly proportional to the increase in the amount of food consumed, particularly in the last two instars. The reason is that not all the food is utilized to promote the growth of the larva. A large amount of food, especially in the last instar, is stored as body fat for utilization in the pupal and adult stages and for the nourishment of the egg cells in the female. The measurements of the width of the head capsule are in agreement with Dyar's rule (*5*), since the increase follows a geometric progression rather closely.

TABLE 7.—*Size of each larval instar of tobacco hornworm reared in the insectary. Quincy, Fla., 1940*

Instar	Larvae measured	Average length of body	Average width of body	Average width of head capsule
	Number	*Mm.*	*Mm.*	*Mm.*
First	50	6.7	0.7	0.8
Second	50	11.2	1.0	1.2
Third	50	23.4	2.4	2.0
Fourth	50	49.0	5.5	3.0
Fifth	35	81.3	11.0	5.0

Larvae were reared in a specially constructed insectary in which the air movement was unrestricted from both ends and one side (fig. 11). Air movement was further increased by constructing the shelves in the form of wooden frames covered with 16-mesh screen wire. The larvae were placed first in inverted jelly glasses, and as their size increased they were transferred to lantern globes covered with cheesecloth. There was probably some air movement into and out of the containers even while they were resting on the shelves, and this helped to keep the larvae in a normal condition.

The larvae were reared on cigar tobacco exclusively. During the early part of the investigations cigar-wrapper tobacco was used, but cigar filler and cigar binder were substituted after a short time, since

the greater thickness and succulence of the leaves of these types elimi-
nated the necessity of placing fresh food into the rearing containers
as frequently as had been necessary when cigar wrapper was used.
The change in types of tobacco produced no observable effects on
the length of the larval period.

Records on the length of the larval period in the insectary are
shown in table 11 (p. 34). The maximum length was 44 days, the

FIGURE 11.—Insectary used in rearing larvae of the tobacco hornworm. A
number of the jelly-glass and lantern-globe rearing containers are shown on
the shelves.

minimum 13, and the average 20. Gilmore (8) gives the maximum as
44 days, the minimum 14.5, and the average 21.5, under Tennessee
conditions, which is in close agreement with the above figures. The
records given in table 11 also agree rather closely with those obtained
in Kentucky by Garman and Jewett (6).

The larvae in the insectary were examined daily, and the date of
molting was determined by the presence of the cast skin and head
capsule, or by the increase in the size of the head. In this manner
complete records were obtained on the length of each stadium. Nor-
mally five instars occurred, but occasionally a sixth instar was
recorded. This condition was reported also by Gilmore (8).

Records on the length of life of the larval instars are summarized

in table 8. It is interesting to note the increasing length of time required for the later instars. This was particularly true of the fifth instar, which averaged nearly twice as long as the others. However, this is to be expected, since the greatest amount of feeding and growth occurs in this instar, as noted.

TABLE 8.—*Average length of life of each larval instar of the tobacco hornworm under insectary conditions. Quincy, Fla., 1936–39*

Year	Brood	Obser-vations	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth[1] instar
		Number	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*
	First	200	3.8	3.0	3.0	3.8	5.6	5.6
1936	Second	128	3.4	2.7	2.7	3.1	5.0	
	Third	57	3.3	2.7	2.4	3.5	7.2	
	First	121	2.9	2.5	2.8	4.0	8.0	6.0
1937	Second	78	2.6	2.3	3.0	4.3	8.0	9.0
	Third	6	4.0	3.2	2.8	5.2	7.3	
	First	145	3.5	3.6	3.8	4.4	6.2	10.0
38	Second	93	3.1	2.8	3.2	4.8	7.9	6.5
19	Third	39	2.9	2.5	2.4	3.6	6.0	
	First	293	3.8	3.1	3.2	3.8	6.8	
39	Second	80	2.9	2.3	2.6	3.2	5.7	
19	Third	68	2.9	2.4	2.9	3.9	7.5	
1936–39	All broods	1,303	3.4	2.9	3.0	3.9	6.6	5.7

[1] The values for this instar were calculated on the basis of the small number of larvae that passed through 6 instars.

RELATIONSHIP OF HUMIDITY AND TEMPERATURE TO LENGTH OF THE LARVAL PERIOD

Larvae in the insectary were exposed to the same general variations in humidity as were described in connection with the discussion on the relationship of this factor to the length of the incubation period. However, the relative humidity within the rearing containers was kept near the saturation point during part of the time by the addition of fresh tobacco leaf, as was evidenced by the condensation of moisture on the inside of the containers. Therefore no accurate record of humidity conditions within the containers is available, but no observable effects of any possible fluctuations on the length of the larval period were noted. On rare occasions, when driving rains partially flooded some of the rearing containers on the insectary shelves, a few of the larvae were drowned, and under extremely dry conditions it was necessary to sprinkle the shelves with water to restore normal activity. Thus susceptibility to extremely wet or arid conditions is apparent. An indirect effect of prolonged periods of high humidity on the larval period was observed. Such conditions appear to favor the prevalence of a bacterial disease which destroys many of the larvae and retards development in mild cases.

The relationship between temperature and the length of the larval period is similar to that existing between temperature and the length of the incubation period. Data showing this relationship were calculated by the same method used in the incubation studies—that is, the mean temperatures were calculated for the average larval periods of each lot of larvae reared. The curves plotted from these data for the seasons of 1936, 1937, 1938, and 1939 are shown in figures 12 and 13.
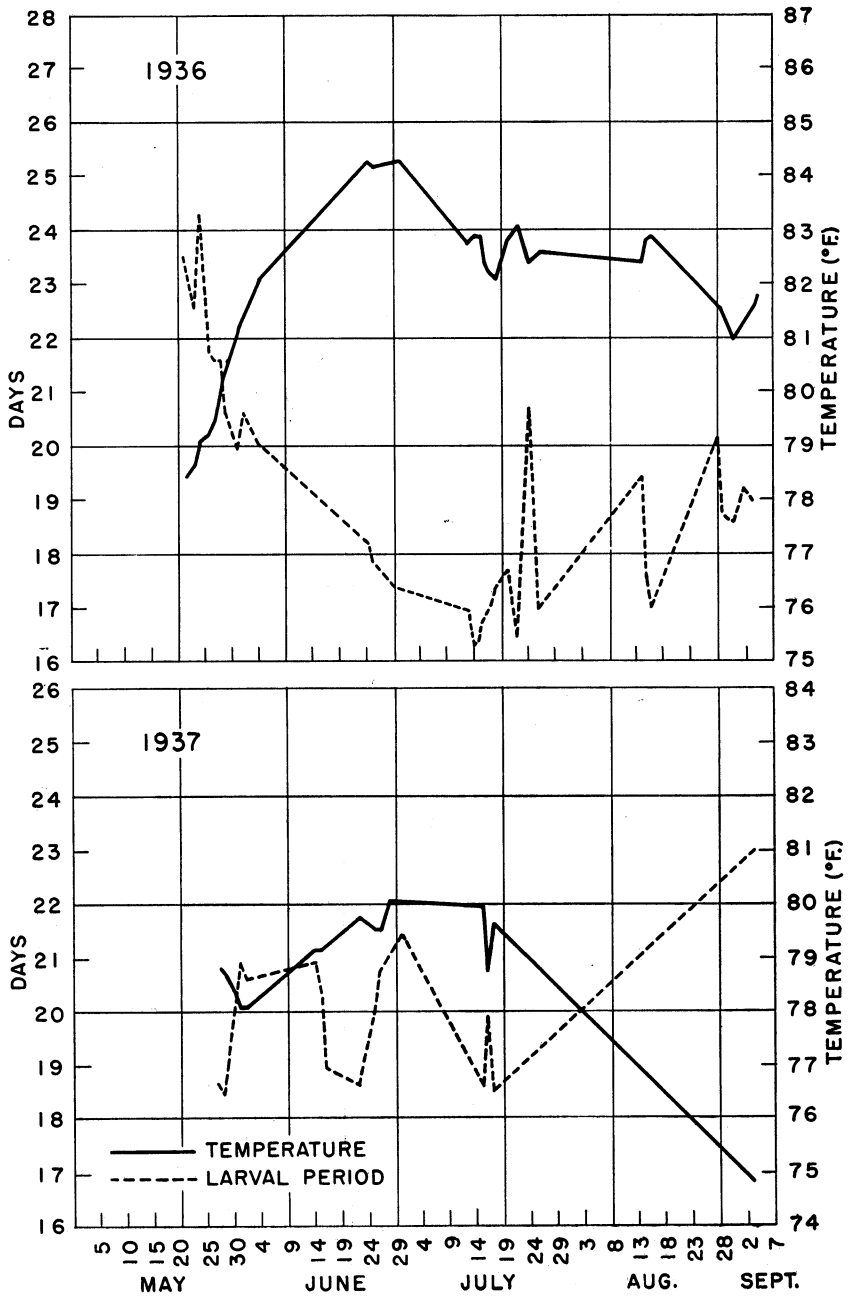
FIGURE 12.—The larval period of the tobacco hornworm as correlated with the temperature. Each point on the temperature curve for a given date represents the mean temperature for the average larval period of larvae hatching on that date. Quincy, Fla., 1936–37.
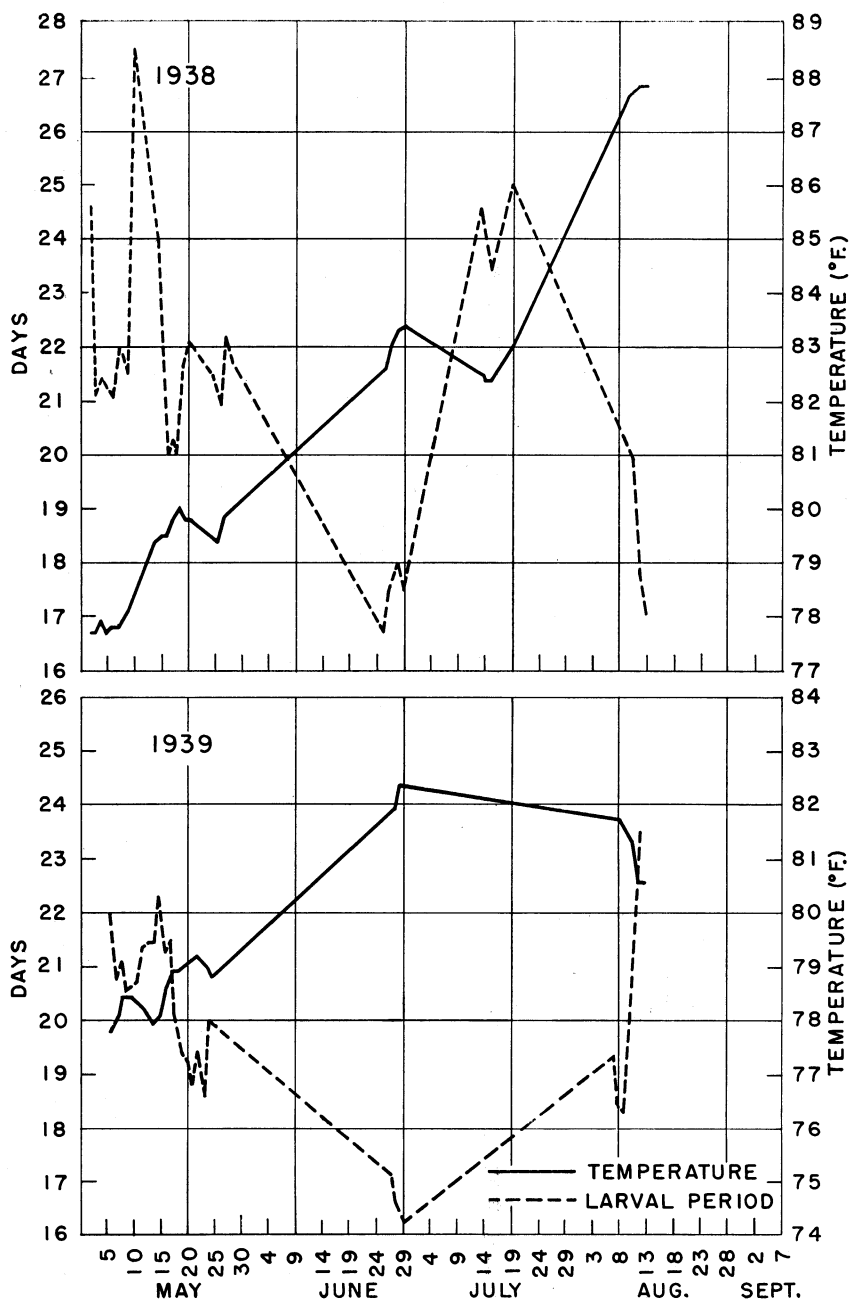
FIGURE 13.—The larval period of the tobacco hornworm as correlated with the temperature. Each point on the temperature curve for a given date represents the mean temperature for the average larval period of larvae hatching on that date. Quincy, Fla., 1938–39.

In 1936 the mean temperature for the average larval periods ranged from 78.4° to 84.3° F. The average length of the larval period ranged from 16.3 to 24.3 days, and this variation is closely related to the temperature range. The correlation coefficient is −0.86, which is highly significant.

In 1937 the mean temperature ranged from 74.8° to 80.1° F., but in the majority of cases it was close to 79°. In spite of the uniformity in mean temperatures, the average larval periods ranged from 18.5 to 23.0 days. This is attributed to the prevalence in the insectary of the bacterial disease mentioned previously, which prolonged the developmental period of some of the larvae beyond the limits imposed by temperature. The correlation coefficient is −0.61, which is significant.

In 1938 the mean temperature ranged from 77.7° to 87.8° F., while the average larval periods ranged from 16.7 to 27.5 days. The correlation coefficient is −0.49, which is highly significant.

In 1939 the mean temperature ranged from 77.8° to 82.3° F., and the average larval periods ranged from 16.2 to 23.5 days. The correlation coefficient is −0.66, which is highly significant.

The complete data for the four seasons indicate that in general an increase of a little more than 1 day in the average length of the larval period may be expected with each degree of decrease in the mean temperature for the developmental period. With a rise in temperature, a corresponding drop in the length of the larval period should occur. Of course this rule will apply only within the limits of normal developmental temperatures.

Length of the Larval Period under Field Conditions

To obtain records on the length of the larval period under more closely simulated field conditions than were afforded by the insectary, it appeared desirable to rear a number of unconfined larvae on tobacco plants in a manner approximating normal developmental conditions. As such rearing could not be conducted in the open because of the activities of natural enemies, it was carried on inside a large, cloth-covered cage (fig. 14), in which conditions were comparable to those existing within a tobacco shade field. The method followed was to divide into two lots a number of larvae emerging on the same date from eggs deposited by the same female. One of these lots was reared in the insectary; the other was reared simultaneously on tobacco plants growing in the cage. In this manner a direct comparison of the lengths of the larval period under both sets of conditions was obtained. A number of such comparisons were made during the seasons of 1936, 1937, 1938, and 1939, and a summary of the results is presented in table 9. It will be noted that the average larval period was 3 days shorter in the cage than it was in the insectary. This is attributed partly to the higher mean temperature in the cage, since, as has already been shown, this factor is closely associated with a decrease in the length of the larval period. However, continuous access to the host plant was probably an additional factor in this case, as in general the temperature differences were not great enough to produce the results recorded.

FIGURE 14.—Large cage in which tobacco hornworm larvae were reared under simulated field conditions.

TABLE 9.—*Comparative length of the larval period of the tobacco hornworm under insectary and cage conditions. Quincy, Fla., 1936–39*

Year	Larvae observed		Average larval period	
	In insectary	In outdoor cage	In insectary	In outdoor cage
	Number	*Number*	*Days*	*Days*
1936	75	26	18	16
1937	13	19	20	15
1938	38	40	22	17
1939	110	45	20	17
1936–39	236	130	19.7	16.5

PUPAL STAGE

After attaining maximum growth the larva ceases to feed; and, when confined, it crawls restlessly about until permitted to enter the ground. At this time the rhythmic pulsations of the dorsal organ are clearly visible through the body integument, probably because the accumulation of fat tissue within the body cavity forces the organ nearer the epidermis. Though usually negatively geotropic, larvae become positively geotropic during this period; and, when free on the host plant, they descend the stem and burrow into the ground. The larvae burrow obliquely into the soil for several inches and there construct earthen cells of sufficient size to provide free air space around the pupae. According to Gilmore (8) these cells average about 1.5 by 3 inches in external measurements.

Records on the depth of pupation of the tobacco hornworm in sandy-clay soil representative of tobacco land in the area are pre-

sented in table 10. These records were obtained by permitting full-grown larvae to burrow in undisturbed soil. After the passage of sufficient time to insure 100 percent pupation, the soil was carefully shaved away vertically with a hand trowel and the depth of each pupa measured. The maximum depth was 9.5 inches, the minimum 1.5, and the average for the seasons of 1936 to 1939, inclusive, was 5.5. These records are representative of the depth of hibernation, since the measurements were made late enough in the season to include the majority of individuals which normally would have overwintered.

TABLE 10.—*Depth of pupation of the tobacco hornworm in sandy clay soil. Quincy, Fla., 1936–39*

Year	Date larvae entered soil for pupation	Observations	Depth of pupation	
			Range	Average
		Number	*Inches*	*Inches*
1936	June 23–24	141	1.5–7.5	4.0
	July 7–8	114	1.5–8.5	4.2
	July 16–17	108	1.5–8.5	5.3
1937	July 23	241	3.0–9.5	6.5
	July 30	172	1.8–9.0	5.8
1938	July 11	98	2.5–9.5	5.9
	August 11	132	3.5–9.0	6.2
1939	July 7	366	2.5–9.0	5.4
	July 28	119	2.2–8.0	4.9
1936–39		1,491	1.5–9.5	5.5

Pupation begins as soon as the pupal cell is completed, the period of transformation between the larval and pupal stages being known as the prepupal period. The length of the prepupal period was determined indirectly by permitting groups of full-grown larvae to burrow into the soil within small areas 2½ feet square. At different intervals these areas were dug up and the numbers of pupae recorded. In this manner records were obtained 1, 2, 3, 4, 5, 6, 7, and 8 days after larvae entered the soil for pupation. A total of 2,727 records were obtained from 1936 to 1939, inclusive, and the percentage of pupation from 1 to 8 days was 0, 0, 0.2, 49, 86, 96, 99, and 100, respectively. This indicates that the prepupal period ranges from 3 to 8 days and averages between 4 and 5 days.

All larvae completing development in the insectary were allowed to pupate in specially constructed cages, which had previously been set in the soil in such a manner that the bottoms were 10 inches below the surface. Each cage was divided into 100 compartments, 5 by 5 inches square (fig. 15), and individual records were kept separate by placing only a single larva in each of these compartments. The date each individual entered the ground and the date of emergence of the adult were recorded, and from these data the length of time between burrowing and emergence was calculated. In this manner records on the length of the pupal period were obtained. These records which include the length of the prepupal period, are summarized in table 11 (p. 34). Since individuals emerging the same and the following season are included, there is a rather wide variation in the length of the period, ranging from a minimum of 14 days to a maximum of 405, with an average of 137.

Although the maximum pupation period was 405 days for insectary-reared material, a much longer maximum was obtained from seasonal-history pupation cages, which were stocked mainly with larvae collected in the field. A limited number of records exceeding 2 years in length were obtained from these cages, the maximum being 738 days.
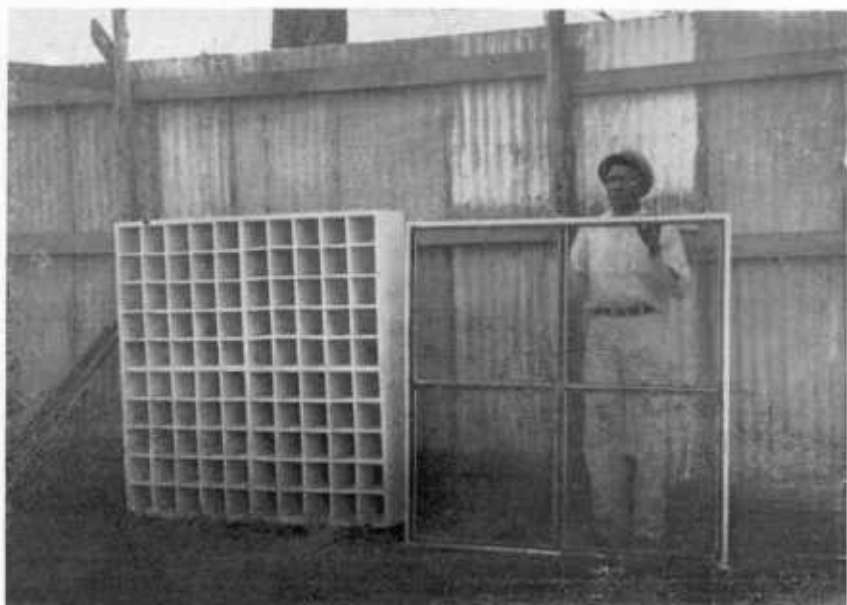

FIGURE 15.—Type of cage used in obtaining records on the length of the pupal period of the tobacco hornworm. The cage is resting on one edge so that each of the individual pupation cells is visible. The screen-wire cover is being held at the right.

Records on the percentage of emergence from overwintering pupae show that a large number of individuals survive the hibernation period. These records are as follows: 1937, 53 percent; 1938, 20 percent; 1939, 24 percent; and 1940, 40 percent. This represents the survival to be expected when protection from parasites is provided, which is the case under insectary and cage conditions. Apparently cold weather is not a factor in winter mortality, since a high percentage of survival occurred in 1940 in spite of the unusually severe winter.

LENGTH OF DEVELOPMENTAL PERIOD

The total length of time required for the completion of development under insectary and cage conditions is shown in table 11. These records, which do not include the preoviposition period, range from a maximum of 441 days to a minimum of 33, with an average of 162. The extremely long hibernation period recorded from the seasonal-history cages indicates that the developmental period may last approximately 2½ years in a limited number of cases.

TABLE 11.—*Length of stages of development of the tobacco hornworm under insectary conditions. Quincy, Fla., 1936–39*

Year and brood	Incubation period			Larval period			Pupal period			Total period of development	
	Obser-vations	Range	Aver-age	Obser-vations	Range	Aver-age	Obser-vations	Range	Aver-age	Range	Aver-age
	Number	*Days*	*Days*	*Number*	*Days*	*Days*	*Number*	*Days*	*Days*	*Days*	*Days*
1936											
First_____	531	3–8	5.5	200	15–26	20	154	20–386	161	38–420	186
Second___	313	2–6	4.4	128	15–25	17	97	22–332	188	39–363	209
Third____	244	3–5	4.3	57	14–25	19	18	233–268	249	250–298	273
1937											
First_____	463	2–7	4.6	121	16–28	20	65	18–342	106	36–377	131
Second___	786	2–8	4.9	78	15–44	20	16	19–310	161	36–362	186
Third____	20	5–7	6.0	6	21–24	22	4	211–257	246	247–288	274
1938											
First_____	312	3–7	4.3	145	18–35	22	115	14–393	118	35–438	144
Second___	558	2–6	4.7	93	15–31	22	55	18–327	134	35–364	161
Third____	310	2–5	4.2	39	14–21	17	18	19–289	228	35–315	249
1939											
First_____	1,042	2–8	5.4	293	16–28	21	217	20–405	99	38–441	125
Second___	809	2–7	4.6	80	13–25	17	59	18–355	51	33–387	73
Third___	242	2–7	4.4	68	16–30	20	36	18–310	280	36–347	304
1936–39, all broods	5,630	2–8	4.9	1,308	13–44	20	854	14–405	137	33–441	162

LONGEVITY OF ADULTS

Longevity records, obtained under cage conditions, on a total of 213 males, range from a minimum of 1 day to a maximum of 19 days, with an average of 6.7. Records on a total of 176 females, under the same environmental conditions, range from a minimum of 1 day to a maximum of 20 days, with an average of 8.8. Thus not only is the maximum life of the female slightly longer, but the average is approximately 2 days longer than that of the male.

SEX RATIO

An indication of the proportions of the sexes was obtained by recording the sex of each individual emerging from the pupation cages. The results from 1936 to 1940, inclusive, are presented in table 12. The sex ratio was 48 percent females. However, as this is practically 50 percent, and on the basis of additional evidence obtained in the field, it is concluded that the numbers of the sexes are approximately equal in nature.

TABLE 12.—*Sex ratio of the tobacco hornworm adults emerging from pupation cages. Quincy, Fla., 1936–40*

Year	Adult emergence	Females
	Number	*Percent*
1936_____	370	50
1937_____	869	48
1938_____	493	48
1939_____	454	46
1940_____	281	48
1936–40 _____	2,467	47.9

SEASONAL HISTORY AND ABUNDANCE

There is considerable confusion in the literature with respect to the proper meaning of the terms "brood" and "generation." Therefore, before taking up a discussion of the seasonal history, it appears desirable to present a definition of these terms in the sense in which they are used in this bulletin. The term "generation" designates all the consecutive stages throughout the season, beginning with the egg and ending with the adult. Thus the first eggs deposited at the beginning of the season would start the first generation, and the resulting larvae, pupae, and adults would all belong to this generation. The term "brood" refers to any stage belonging to a specific generation or to an unknown generation. For example, the eggs, larvae, pupae, and adults belonging to the first generation are first-brood eggs, larvae, pupae, or adults. The first adults of the season, which emerge from overwintering pupae, are designated as "spring-brood adults," since they do not belong to a specific generation. This follows the definitions given by Yothers and Van Leeuwen (*32*), who use the terminology adopted by the Bureau of Entomology for a number of publications on the life history of the codling moth.

Data on the seasonal history and abundance of the tobacco hornworm were obtained from the life-history studies, cage and moth-trap records, and general field observations. In this way more accurate and comprehensive information was obtained than if the life-history records had been considered exclusively.

SEASONAL RANGE

As has already been stated, the tobacco hornworm spends the winter in the pupal stage several inches beneath the surface of the soil. A rather long series of records are available on the earliest and latest appearances of the three other stages in the southern cigar-tobacco district. These records present a general conception of the seasonal range of the species in this area.

The first stage to appear in the spring is the adult, and although the records indicate some variation in the date of this occurrence, it is generally from the middle to the latter part of April. These moths emerge just in time to deposit their eggs on newly transplanted tobacco. The last stages recorded in the fall are usually the egg or larval stages. These records are obtained around the latter part of October or the first of November. The first severe frost of the season destroys all individuals remaining in the field. Late-appearing adults and larvae are merely stragglers, as there is a sharp decline in abundance after about the middle of August, or directly following the harvesting of the tobacco crop.

NUMBER OF GENERATIONS

Field observations and life-history data show that there are three complete generations and one partial generation each season. Under favorable conditions, however, it is possible that the fourth generation may be completed by a limited number of individuals. The average emergence date of spring-brood adults is about April 20. These moths deposit the first-brood eggs, which begin hatching about

the end of the month. The larval period at this time of the year requires approximately 3 weeks and the pupal period 25 days, so the first generation is completed about June 12. The second generation requires about 47 days and is completed about August 2. The third generation is completed about September 16, thus allowing sufficient time for the completion of a fourth generation before the advent of cold weather. However, the larval period of the fourth generation may be prolonged by such factors as scarcity and poor quality of food, cool nights, and dry weather, so that normally only the pupal stage is reached. Quaintance (*22*, *p. 158*) states that it is possible that four generations do occur in Florida.

Figure 16 is a chart of the seasonal history and abundance. It will be noted that some overlapping of generations takes place, thus making it practically impossible to distinguish between broods after the passage of the first few weeks of the season. The chart gives the approximate normal occurrence and duration of broods, since variations of several weeks earlier or later may take place, depending on weather.

SEASONAL ABUNDANCE

Data on seasonal abundance were obtained from counts of eggs in the field, emergence-cage and trap records, and general observations.

Field counts of eggs during the seasons of 1937, 1938, and 1939 show that there is a gradual increase in the abundance of eggs from the beginning of the season until about the middle of June. There is frequently a slight drop in abundance during the latter part of June, followed by another peak about the first or middle of July. General observations in neglected tobacco fields and on other host plants indicate that egg abundance does not remain at a very high level after about the first of August.

Field observations indicate that larval abundance follows about the same fluctuations as were recorded for egg abundance, although obviously the increases and decreases are somewhat later in most cases.

Adult abundance was determined by trapping. A series of six traps of the type shown in figure 17 were operated during the seasons of 1937, 1938, 1939, and 1940. Iso-amyl salicylate was used as the attractant, and the traps were arranged in a rough circle covering approximately 12 square miles near the center of the tobacco district. The traps were at least 2 miles apart, and the same locations were used each season.

The trap records agree very closely with the egg counts from the field. The catch increases gradually from the first of the season to the early part of June. After this time there is usually a sharp decline in the numbers. This may occur during the latter part of June or in July, depending upon weather conditions. The drop in abundance probably indicates a slight interval between the occurrence of spring-brood and first-brood adults. Invariably an abrupt reduction in numbers occurs sometime between the latter part of July and the middle of August, and a gradual decrease takes place thereafter to the end of the season.
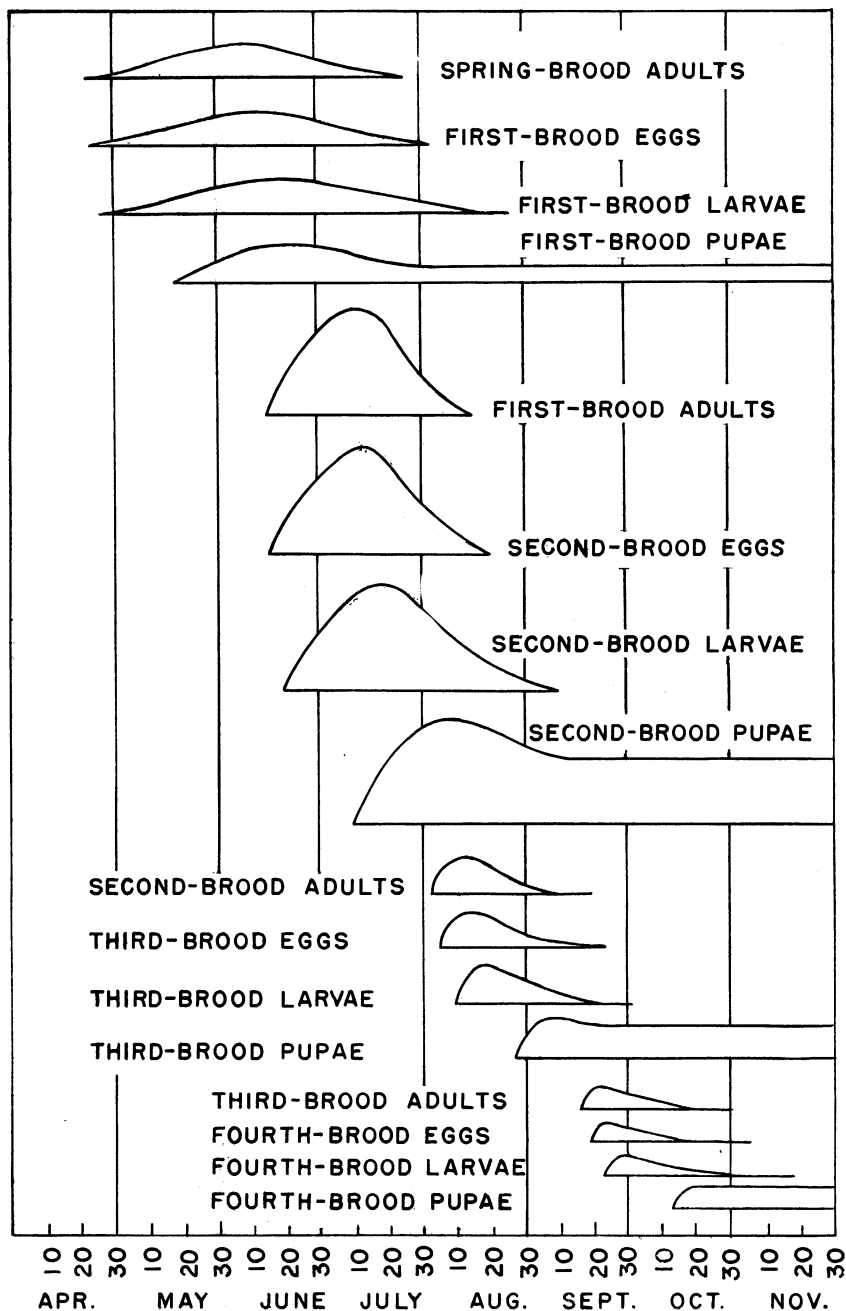
FIGURE 16.—The occurrence, duration, number, and abundance of the broods of the tobacco hornworm at Quincy, Fla. Depth of figures indicates relative abundance.
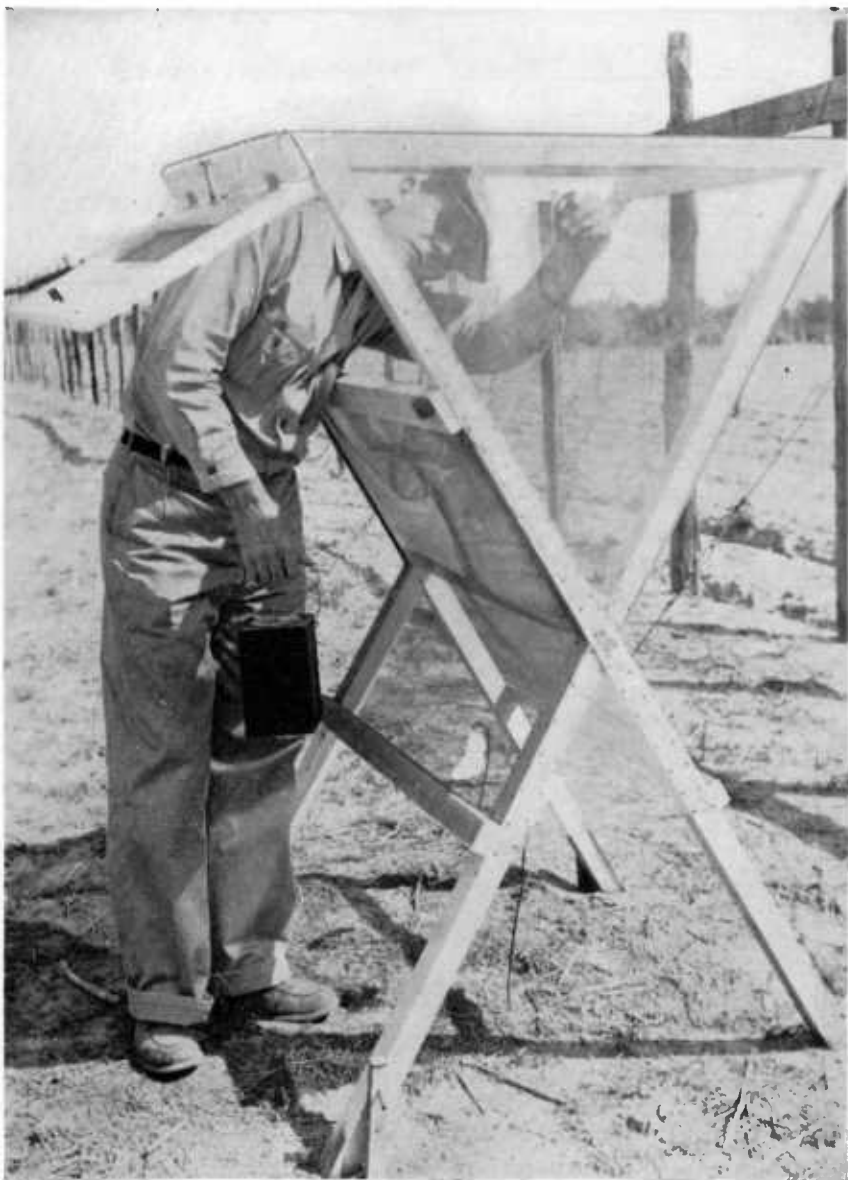
FIGURE 17.—Type of trap used in determining the seasonal abundance of adults of the tobacco hornworm.

The greatest numbers of eggs and larvae occur in the first and second broods, the number in the second brood being nearly twice as great as in the first. This is due to the increasing number of adults and the greater egg-laying potential existing during that part of the season. The third brood is usually much smaller than the second, and the fourth brood is relatively minute.

The principal reason for the sharp decrease in abundance of eggs, larvae, and adults after the first of August appears to be the marked reduction in the percentage of pupae transforming to adults. This was studied in a series of emergence cages which were established each season from 1936 to 1939, inclusive. These cages were 2½ feet square and 3 feet deep. The sides of the lower half of each cage were covered with screen wire, the upper half with cloth, and the top with a screen-wire cover. The cages were set into the ground to a depth corresponding to the section covered with screen wire (fig. 18). At 10-day intervals throughout the season, 75 full-grown larvae were allowed to pupate in the soil within one of these cages.

FIGURE. 18.—Emergence cages used in connection with a study of the seasonal abundance of the tobacco hornworm.

In this manner a representative sample was obtained of each brood occurring in nature, since the majority of the larvae were collected in the field. The results are shown in figure 19. The points on the curves represent the percentages of adults emerging during the same season from larvae which entered the ground for pupation on a given date. It will be noted that reduction in emergence generally began with the larval group entering the soil around the middle or latter part of June, and that there was little or no emergence from larvae entering the soil after August 9.

It would be logical to expect that the decline and termination of adult emergence are related to a reduction in temperature and rainfall. However, there is no evidence to show that such a relationship exists. Moth-trap records showing the fluctuation in abundance of adults during the seasons of 1937 to 1940, inclusive, in relation
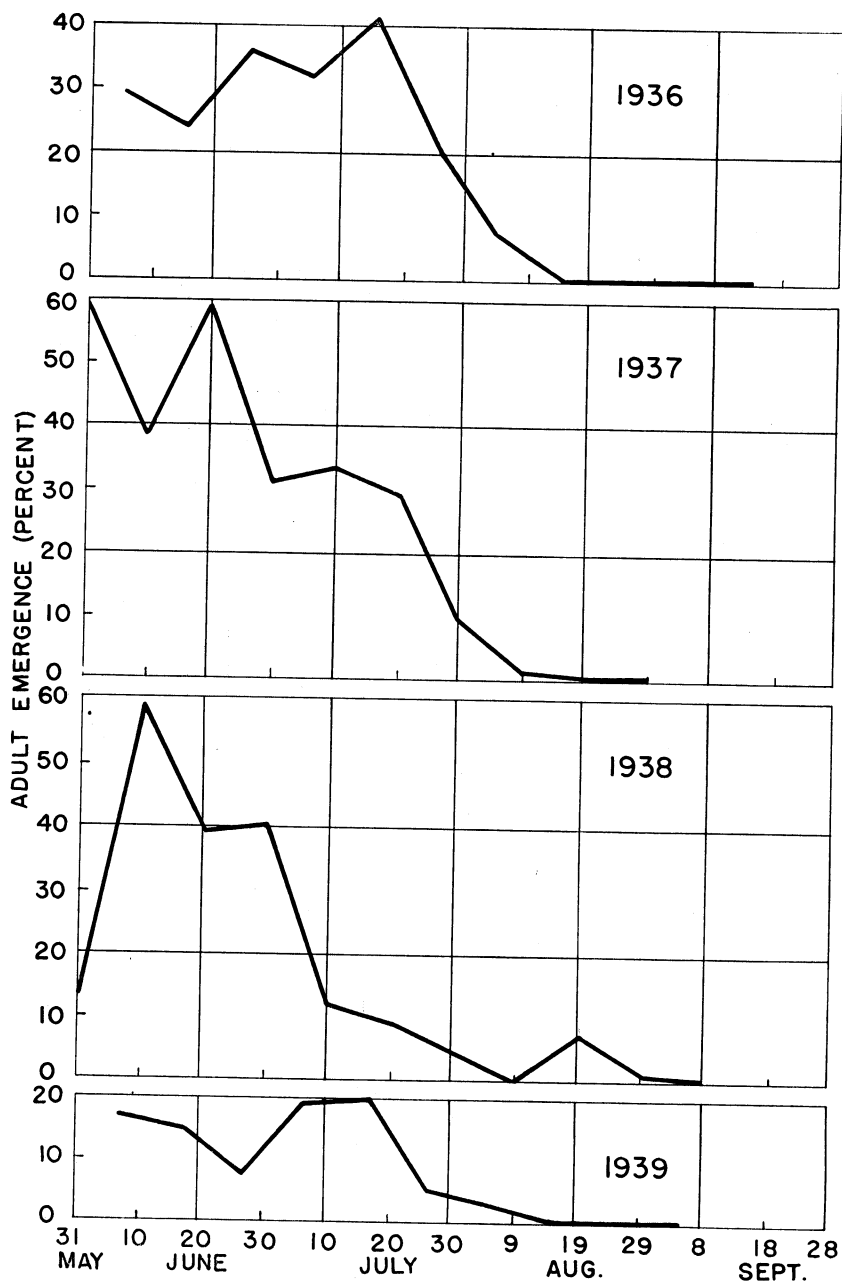
FIGURE 19.—Seasonal reduction in emergence of adults of the tobacco horn-worm. Each point on the curves represents the percentage of adults emerging during the same season from larvae which entered the ground for pupation on a given date.
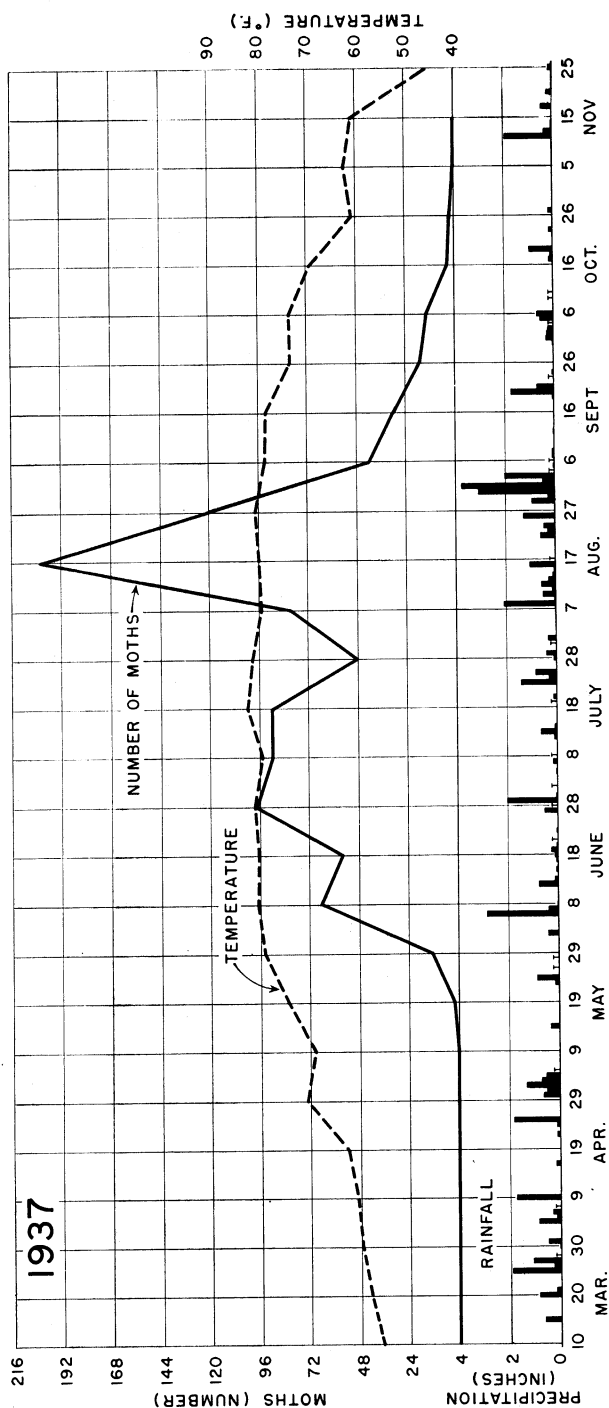
FIGURE 20.—Seasonal abundance of adults of the tobacco hornworm in relation to temperature and rainfall. Quincy, Fla., 1937.
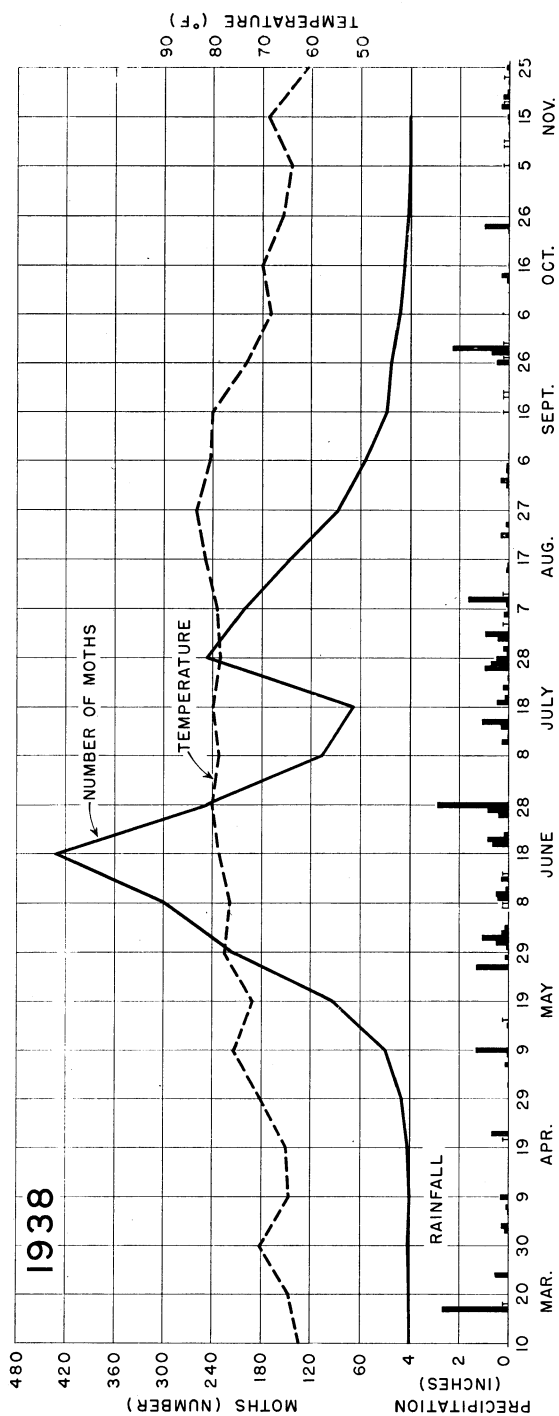
FIGURE 21.—Seasonal abundance of adults of the tobacco hornworm in relation to temperature and rainfall. Quincy. Fla.. 1938.
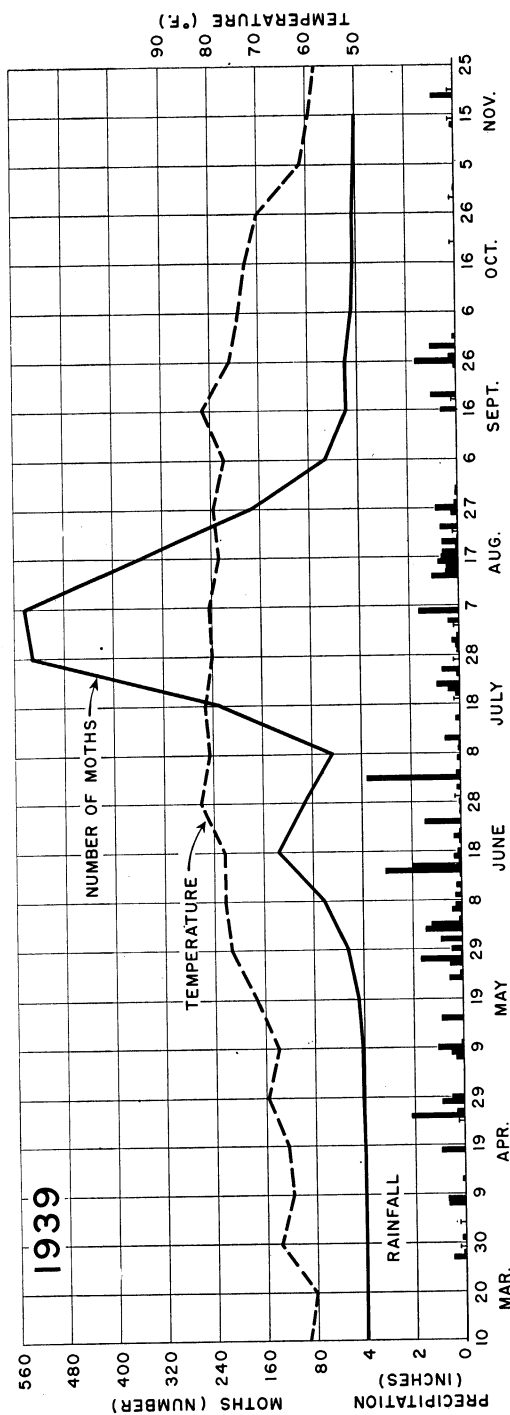
FIGURE 22.—Seasonal abundance of adults of the tobacco hornworm in relation to temperature and rainfall. Quincy, Fla., 1939.
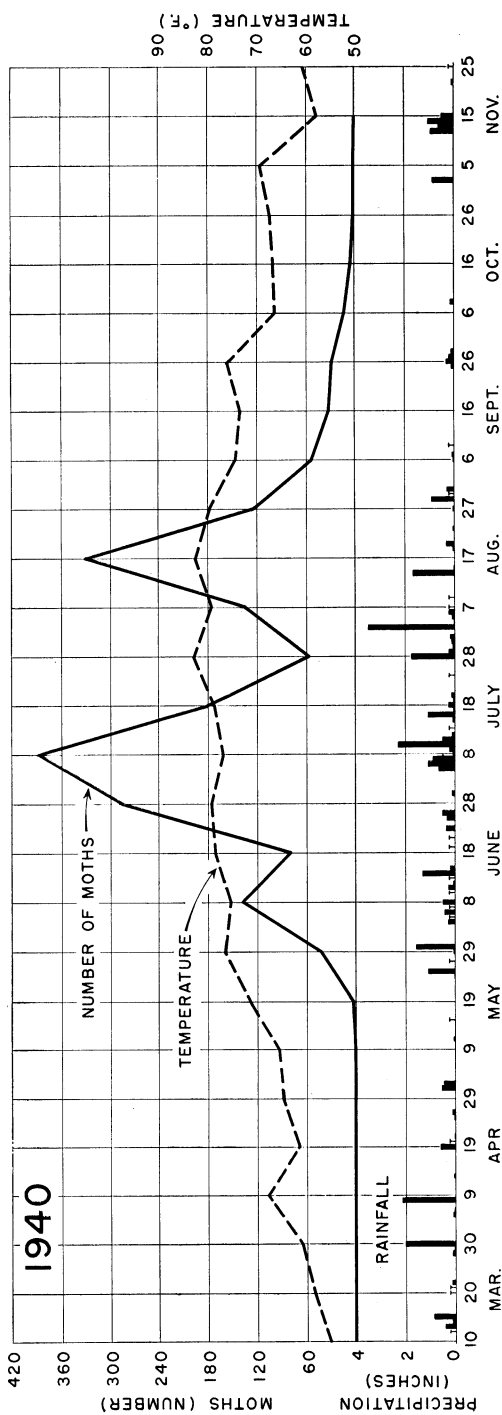
FIGURE 23.—Seasonal abundance of adults of the tobacco hornworm in relation to temperature and rainfall. Quincy, Fla., 1940.

to temperature and precipitation are presented graphically in figures 20–23.

In 1937 no moths were taken before the 10-day period May 9 to 19, although rainfall was sufficient to soften the soil for emergence. Apparently unusually low temperatures up to about the latter part of April were responsible for the delay. Precipitation and temperature remained fairly constant until after September 6, with an abundance of rainfall during the latter part of August and the first of September. Nevertheless, the moth-trap catch dropped abruptly after August 17, indicating that a decrease in adult emergence occurred sometime before that date.

In 1938 the temperature and rainfall were favorable for early emergence and the first record was obtained between March 20 and 30. No marked decrease in temperature occurred until after the middle of September, and there was plenty of rain throughout almost the entire season. In spite of these favorable conditions, however, there was a sharp drop in the moth catch beginning on July 28 and continuing downward almost in a straight line until about the middle of August.

In 1939 the temperature was not very low, but there was a limited amount of rainfall prior to April 18. Under these conditions the first moths appeared between April 19 and 29. The temperature drop at the end of the season did not begin until about the middle of September, while there was plenty of rain up to the first of October. However, the moth-trap catch dropped abruptly after August 7 and continued downward until September 6, indicating that there was little emergence after the middle of August.

In 1940 emergence apparently was retarded by low temperatures, and the first records were not obtained until between May 9 and 19. There was no marked drop in temperature until about the latter part of September, and rainfall was plentiful until September 10. The final drop in the catch, however, began shortly after August 17 and continued until about the first of September.

It may be seen from these records that while temperature and rainfall apparently are important factors in the emergence of adults during the early part of the season, they are not related to the unseasonable termination of emergence during the latter part of the summer and in early fall. Although the cause of the abrupt termination of adult emergence is not clear, the result is that there is a close synchronization between the seasonal history of the hornworm and the tobacco-growing season.

NATURAL ENEMIES

PREDATORS

A number of insect predators of the tobacco hornworm are recorded in the literature. Gilmore (8) lists *Chrysopa rufilabris* Burm. and *Geocoris punctipes* Say as egg predators, *Chrysopa rufilabris*, *Polistes* sp., and *Calathus opaculus* Lec. as larval predators, and *Megaselia nigriceps* (Loew) as a predator of the pupa. None of these species are known to occur in the southern cigar-tobacco district. *Polistes fuscatus* (F.)[8] and *P. fuscatus* var. *metricus* Say[8]

Determined by G. A. Sandhouse.

were the most important predators observed, but it is not known whether either of these is the species referred to by Gilmore. *Polistes fuscatus* var. *metricus* is active mainly during the early part of the season and feeds on all larval instars up to the fourth. In a few cases it was observed that this predator represented the chief factor in the control of hornworms in open fields of tobacco.

A small green spider, *Peucetia viridans* (Hentz), is an important predator, but it is abundant only during the first few months of the season. It attacks the egg and the first three larval instars. A small plant bug, *Cyrtopeltis varians* (Dist.),[9] also preys upon the eggs and larvae, occasionally attacking the fourth and fifth instars. However, it is probably capable of destroying only the egg and first three instars.

A number of common birds, including sparrows, cardinals, mockingbirds, and blue jays, attack the larvae and have been observed to feed freely on pupae and adults when these stages have been made available to them. Moths released during the daytime usually were captured before they could fly 50 yards. It appears probable that the protective coloring, habits of concealment, and nocturnal activities of the species may have been developed mainly as a defense against the attacks of bird enemies.

Skunks and moles feed on the pupae, and records have been obtained of the destruction of large numbers by these animals. Skunks also killed a large number of trapped adults during control experiments conducted in 1941.

PARASITES

Records obtained at the Quincy laboratory on dipterous parasites of the larva of the tobacco hornworm extend back to about 1919. These early records indicate that the following species were important: *Sarcophaga lambens* Wied. (= *sternodontis* (Towns.)), *S. sarracenioides* Ald., *S. rapax* Walk., and *Sturmia protoparcis* (Towns.).[10] In the early 1930's *Sturmia protoparcis* [11] was first recorded and since that time it apparently has become the dominant species. From May 1937 to June 1941, 28 lots of specimens of dipterous parasites reared from the tobacco hornworm or observed attacking it in the field were submitted to the Division of Insect Identification of this Bureau, in Washington, D. C., for positive determination, and all these specimens were identified as *Sturmia protoparcis*.[11] Only one other dipterous parasite, *Sarcophaga rapax* Walk.,[11] was reared from the hornworm during this entire period.

Sturmia protoparcis has been observed in the field from the first of May until the latter part of September, but the peak of abundance usually is reached during August. The fly deposits minute, whitish, elongate-oval eggs on the body of the hornworm larva. These eggs are approximately 0.9 mm. long and 0.2 mm. wide. They are cemented to various parts of the body of the host by lightning-like motions of the ovipositor, and they hatch almost immediately. In hatching, the larva emerges from the egg through the side

[9] Determined by H. G. Barber.
[10] The late J. M. Aldrich determined this as *Sturmia distincta* (Wied.), but it has been found that the *S. distincta* of American authors is not the true *distincta* of Wiedemann.
[11] Determinations by D. G. Hall.

attached to the body of the host and burrows directly into the host integument. The hornworm larva uses its mouth parts in attempting to dislodge all eggs deposited on accessible portions of its body, and observations indicate that the parasite is unable to penetrate the epidermis of the host if such attempts are successful, although emergence from the egg takes place. Evidently it is only when the egg is anchored firmly to the body wall of the host that the parasite obtains the necessary mechanical advantage to carry on its burrowing activities.

Usually only fifth-instar larvae are attacked, and these larvae are capable of completing their development and burrowing into the soil for pupation. The parasite completes its development within the body of the host and emerges from the ground as an adult.

Third- and fourth-brood larvae of the tobacco hornworm generally are parasitized rather heavily by *Sturmia protoparcis*, and this causes an appreciable reduction in the number of spring-brood adults emerging the following season.

The small braconid wasp *Apanteles congregatus* (Say) is considered one of the most important parasites of the tobacco hornworm, and Gilmore (*9*) states that *Protoparce sexta* is the preferred host. However, few records of parasitization by this species have been obtained in the Southern cigar-tobacco district, except possibly by Quaintance (*22*), who states that it is an important enemy of the hornworm in Florida. Thousands of hornworm larvae were collected in the field during the period 1936 to 1939, but only three records of parasitization by *Apanteles* were obtained.

The reason for such a scarcity of this parasite in the area is not clear. Marcovitch and Stanley (*20, p. 5*) state that its activities are hampered by the sticky gums on tobacco leaves, and, according to Gilmore (*9*), although parasitization was heavy on larvae feeding on tomatoes, there was practically no possibility for *Apanteles* to complete its development on larvae reared on dark-fired tobacco. This might offer an explanation for the scarcity of *Apanteles* in the southern cigar-tobacco district, since the early records of the Quincy laboratory indicate that parasitization of larvae collected from jimsonweed (*Datura* spp.) or tomato was not uncommon. However, two of the records between 1936 and 1939 were obtained from larvae feeding on tobacco, and observation and collection of larvae on jimsonweed and tomato failed to show any increase in the incidence of parasitization by *Apanteles*. A record of hyperparasitization by *Hypopteromalus tabacum* (Fitch) was obtained in 1926, but since no further records have been obtained it is apparent that this is not the cause of the scarcity of *Apanteles*. It is evident that certain factors are in operation which tend to prevent the establishment of *Apanteles* in the area, although the identity of these factors still remains to be determined.

A record of an egg parasite of the tobacco hornworm was obtained at the Quincy laboratory in 1917 by F. L. McDonnough. Twelve small parasites, tentatively identified as serphids, issued from an egg collected on jimsonweed (*Datura stramonium*). The specimens were sent to Washington for determination, but unfortunately were lost in transit. The species apparently was unable to establish itself, as no egg parasites have been recorded since that time.

Gilmore (*8*) lists *Telenomus nigriscapus* Ashm., *Trichogramma minutum* Riley, and *Telenomus sphingis* Ashm. (= *monilicornis* Ashm.) as egg parasites; *Sturmia incompta* (V. d. W.), *S. protoparcis* (Towns.), *Sarcophaga rapax* Walk., *Winthemia quadripustulata* (F.), *Carcelia amplexa* Coq., *Euplectrus plathypenae* Howard, and *Apanteles congregatus* (Say) as larval parasites; and *Sturmia protoparcis* (Towns.), *Winthemia quadripustulata* (F.), and *Sarcophaga* spp. as parasites of the pupa, although it is doubtful whether the last three species ever actually parasitize the hornworm in the pupal stage.

DISEASE

A bacterial disease of the larva of the tobacco hornworm usually is present in the field during the latter part of the tobacco-growing season. The symptoms of this disease agree in general with those of hornworm septicemia, which is caused by *Bacillus sphingidis* White. These symptoms are described by White (*30*). There are, however, a number of similar organisms in the bacterial group causing diseases of this type, and the causal organism may not be the same in this case. Cultures from diseased larvae were sent to White for identification of the organism, and the following report was received: "Examination of the culture of tube No. 2 shows it to be a bacillus of the septicemia group. The species of this group are very closely related and are not readily distinguished. The disease is apparently hornworm septicemia . . ." [12]

Larvae affected by the disease lose their appetites, and the droppings become watery and dirty white. The turgidity of the body often is lost, and the larva becomes flabby. The bodies of dead specimens turn brown and then black, and the skin stretches so that the body often attains twice its normal length. Dead larvae usually hang head downward from the under side of the tobacco leaf (fig. 24).

The disease appears about the first of June and increases rapidly during the hottest weather, reaching a peak in August. The increase seems to be favored by frequent rains, since hot, humid weather provides optimum conditions for the development of the causal organism. After the first of September the disease disappears. This is probably because of the slightly cooler and drier weather.

During the 1938 season, 45 affected larvae were studied rather closely in the insectary. Most of these larvae were of the fourth or fifth instar. They were provided with fresh food and examined twice daily until death occurred. In all cases the characteristic symptoms were noted. The average period of survival was 2.6 days, with a minimum of a fraction of a day and a maximum of 9 days. Two individuals completed development and entered the ground for pupation, one later emerging as an adult male. This male was only about one-half normal size but seemed active and lived several days. It appears, therefore, that some individuals may survive even severe attacks, and probably many mild cases exhibit no outward indications other than an abnormal lengthening of the developmental period.

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[12] Extract from a letter received from G. F. White through W. H. White, October 16, 1936.

Although the disease was very prevalent under cage and insectary conditions, this was not often the case in the field. Thus its value in control is questionable. The method of transmission is unknown.

FIGURE 24.—Larva of the tobacco hornworm killed by hornworm septicemia.

In general, natural enemies of the tobacco hornworm are of little direct importance in the control of this pest on cigar tobacco. Because of the nature of the crop, severe damage will have occurred before control by natural enemies could be obtained. However, natural enemies are of much value indirectly, in that they serve as a limiting factor to the hornworm population in the area.

LITERATURE CITED

(1) ALWOOD, W. B.
    1898. ON THE LIFE HISTORY OF PROTOPARCE CAROLINA. *In* Proceedings of the Tenth Annual Meeting of the Association of Economic Entomologists, U. S. Dept. Agr., Div. Ent. Bul. (n. s.) 17, pp. 72–74.

(2) BURMEISTER, H.
    1856. SYSTEMATISCHE UEBERSICHT DER SPHINGIDAE BRASILIENS. 17 pp. Halle. (Abhandl. Naturf. gesell. Halle, Vierteljahrsbericht, t. 3, Sitzungsber., pp. 58–75.)

(3) BUTLER, A. G.
    1877. REVISION OF THE HETEROCEROUS LEPIDOPTERA OF THE FAMILY SPHINGIDAE. [London] Zool. Soc. Trans. 9: 511–644, illus.

(4) CORNELL UNIVERSITY AGRICULTURAL EXPERIMENT STATION.
    1928. A LIST OF THE INSECTS OF NEW YORK, WITH A LIST OF THE SPIDERS AND CERTAIN OTHER ALLIED GROUPS. N. Y. (Cornell), Agr. Expt. Sta. Mem. 101 (1926), 1121 pp., illus.

(5) DYAR, H. G.
    1890. THE NUMBER OF MOLTS OF LEPIDOPTEROUS LARVAE. Psyche 5: 420–422.

(6) GARMAN, H., and JEWETT, H. H.
    1920. THE BROODS OF THE TOBACCO WORMS. Ky. Agr. Expt. Sta. Bul. 225, 24 pp., illus.

(7) GARNER, W. W., MOSS, E. G., YOHE, H. S., and others.
    1923. HISTORY AND STATUS OF TOBACCO CULTURE. U. S. Dept. Agr. Yearbook 1922: 395–468, illus.

(8) GILMORE, J. U.
    1938. OBSERVATIONS ON THE HORNWORMS ATTACKING TOBACCO IN TENNESSEE AND KENTUCKY. Jour. Econ. Ent. 31: 706–712.

(9) ———
    1938. NOTES ON APANTELES CONGREGATUS (SAY) AS A PARASITE OF TOBACCO HORNWORMS. Jour. Econ. Ent. 31: 712–715, illus.

(10) GLOVER, T.
    1856. INSECTS FREQUENTING THE COTTON-PLANT. U. S. Commr. Pat. Rpt. 1855: 64–119.

(11) HENDERSON, J. R.
    1939. THE SOILS OF FLORIDA. Fla. Agr. Expt. Sta. Bul. 334, 67 pp., illus.

(12) HOFFMANN, C. C.
    1942. CATALOGO SISTEMATICO Y ZOOGEOGRAFICO DE LOS LEPIDOPTEROS MEXICANOS. TERCERA PARTE. SPHINGOIDEA Y SATURNIOIDEA. [Mex.] Univ. Nac., Inst. de Biol. An. 13: [213]–256.

(13) HÜBNER, J.
    1819. VERZEICHNISS BEKANNTER SCHMETTLINGE. 431 pp. Augsburg.

(14) HYSLOP, J. A.
    1938. LOSSES OCCASIONED BY INSECTS, MITES, AND TICKS IN THE UNITED STATES. U. S. Bur. Ent. and Plant Quar. E–444, 57 pp. [Processed.]

(15) JOHANSSON, B.
    1763. CENTURIA INSECTORUM RARIORUM. 32 pp. Upsaliae (Uppsala), Sweden.

(16) LINNAEUS, C.
    1758. SYSTEMA NATURÆ. Ed. 10, t. 1. 824 pp. Holmiæ.

(17) ——
1764. MUSEUM LUDOVICÆ ULRICÆ. [722] pp. Holmiæ.

(18) LINTNER, J. A.
1864. NOTES ON SOME SPHINGIDAE OF THE STATE OF NEW YORK, WITH DESCRIPTIONS OF THEIR LARVAE AND PUPAE. Phila. Ent. Soc. Proc. 3 : 645–672.

(19) MADDEN, A. H., and CHAMBERLIN, F. S.
1938. BIOLOGICAL STUDIES OF THE TOMATO WORM ON TOBACCO IN FLORIDA, 1936 AND 1937. Jour. Econ. Ent. 31 · 703–706.

(20) MARCOVITCH, S., and STANLEY, W. W.
1937. CONTROL OF TOBACCO INSECTS IN TENNESSEE. Tenn. Agr. Expt. Sta. Bul. 160, 14 pp., illus.

(21) MERRIAM, C. H.
1898. LIFE ZONES AND CROP ZONES OF THE UNITED STATES. U. S. Dept. Agr., Div. Biol. Survey Bul. 10, 79 pp., illus.

(22) QUAINTANCE, A. L.
1898. A PRELIMINARY REPORT UPON THE INSECT ENEMIES OF TOBACCO IN FLORIDA. Fla. Agr. Expt. Sta. Bul. 48 : [154]–188, illus.

(23) ROTHSCHILD, W., and JORDAN, K.
1903. A REVISION OF THE LEPIDOPTEROUS FAMILY SPHINGIDAE. Novitates Zool. 9 [2 pts.], 972 pp., illus.

(24) SMALL, J. K.
1933. MANUAL OF THE SOUTHEASTERN FLORA. 1554 pp., illus. New York.

(25) STOUTAMIRE, R.
1936. TOBACCO GROWING IN FLORIDA. (Revised by C. P. Helfenstein.) Fla. Dept. Agr. Bul. (n. s.) 40, 45 pp., illus.

(26) TISDALE, W. B.
1928. TOBACCO CULTURE IN FLORIDA. Fla. Agr. Expt. Sta. Bul. 198, pp. 378–428, illus.

(27) UNITED STATES DEPARTMENT OF AGRICULTURE.
1943. AGRICULTURAL STATISICS 1943. 548 pp. Washington, D. C.

(28) WAGNER, H.
1913. SPHINGIDAE: SUBFAMILY ACHERONTIINAE. In his Lepidopterorum Catalogus. Pars 12, 77 pp. Berlin.

(29) WEBSTER, F. M.
1904. DIFFUSION OF THE HAWK MOTHS IN NORTH AMERICA. Canad. Ent. 36 : 65–69, illus.

(30) WHITE, G. F.
1923. HORNWORM SEPTICEMIA. Jour. Agr. Res. 26 : 477–486, illus.

(31) WYCKOFF, V. J.
1936. TOBACCO REGULATION IN COLONIAL MARYLAND. 228 pp. Baltimore.

(32) YOTHERS, M. A., and VAN LEEUWEN, E. R.
1931. LIFE HISTORY OF THE CODLING MOTH IN THE ROGUE RIVER VALLEY OF OREGON. U. S. Dept. Agr. Tech. Bul. 255, 34 pp., illus.